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THE Committee appointed by the *Royal Society* to direct the publication of the *Philosophical Transactions* take this opportunity to acquaint the public that it fully appears, as well from the Council-books and Journals of the Society as from repeated declarations which have been made in several former *Transactions*, that the printing of them was always, from time to time, the single act of the respective Secretaries till the Forty-seventh Volume; the Society, as a Body, never interesting themselves any further in their publication than by occasionally recommending the revival of them to some of their Secretaries, when, from the particular circumstances of their affairs, the *Transactions* had happened for any length of time to be intermitted. And this seems principally to have been done with a view to satisfy the public that their usual meetings were then continued, for the improvement of knowledge and benefit of mankind: the great ends of their first institution by the Royal Charters, and which they have ever since steadily pursued.

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1894.

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Italy (continued).

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  - *p.* University.
- Pisa.
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- Luxembourg.
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Malta.

- *p.* Public Library.

Mauritius.

- *p.* Royal Society of Arts and Sciences.

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  - *p.* École Polytechnique.
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  - AB. Provinciaal Genootschap van Kunsten en Wetenschappen.

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  - AB. New Zealand Institute.

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- Christiania.
  - AB. Kongelige Norske Frederiks Universitet.
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  - *p.* Museum.
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  - AB. Kongelige Norske Videnskabers Selskab.

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  - AB. Le Musée Public.
  - B. Société Impériale des Naturalistes.
- Odessa.
  - *p.* Société des Naturalistes de la Nouvelle-Russie.
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- St. Petersburg.
  - AB. Académie Impériale des Sciences.

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  - AB. Comité Géologique.
  - *p.* Compass Observatory.
  - A. Observatoire Physique Central.

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  - AB. University.
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  - A. Royal Observatory.
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  - AB. Royal Society.
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  - *p.* Philosophical Society.

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  - A. Circolo Matematico.
  - AB. Consiglio di Perfezionamento (Società di Scienze Naturali ed Economiche).
  - Reale Osservatorio.

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  - A. Instituto y Observatorio de Marina de San Fernando.
- Madrid.
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  - AB. Real Academia de Ciencias.

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  - AB. Kongl. Vetenskaps och Vitterhets Samhälle.
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Geneva.
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Lausanne.
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Tasmania.

Hobart.
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Chicago.
- AB. Academy of Sciences.
- *p.* Journal of Comparative Neurology.

United States (continued).

Davenport (Iowa).
- *p.* Academy of Natural Sciences.

Madison.
- *p.* Wisconsin Academy of Sciences.

Mount Hamilton (California).
- A. Lick Observatory.

New Haven (Conn.).
- AB. American Journal of Science.
- AB. Connecticut Academy of Arts and Sciences.

New York.
- *p.* American Geographical Society.
- *p.* American Museum of Natural History.
- *p.* New York Academy of Sciences.
- *p.* New York Medical Journal.
- *p.* School of Mines, Columbia College.

Philadelphia.
- AB. Academy of Natural Sciences.
- AB. American Philosophical Society.
- *p.* Franklin Institute.
- *p.* Wagner Free Institute of Science.

Rochester (N.Y.).
- *p.* Academy of Science.

St. Louis.
- *p.* Academy of Science.

Salem (Mass.).
- *p.* American Association for the Advancement of Science.
- AB. Essex Institute.

San Francisco.
- AB. California Academy of Sciences.

Washington.
- AB. Patent Office.
- AB. Smithsonian Institution.
- AB. United States Coast Survey.
- *p.* United States Commission of Fish and Fisheries.
- AB. United States Geological Survey.
- AB. United States Naval Observatory.
- *p.* United States Department of Agriculture.
- A. United States Department of Agriculture (Weather Bureau).

West Point (N.Y.)
- AB. United States Military Academy.

ADJUDICATION of the MEDALS of the ROYAL SOCIETY for the year 1893, by the PRESIDENT and COUNCIL.

The COPLEY MEDAL to Sir GEORGE GABRIEL STOKES, Bart., F.R.S., for his Researches and Discoveries in Physical Science.

A ROYAL MEDAL to ARTHUR SCHUSTER, F.R.S., for his Spectroscopic Inquiries, and his Researches on Disruptive Discharge through Gases, and on Terrestrial Magnetism.

A ROYAL MEDAL to HARRY MARSHALL WARD, F.R.S., for his Researches into the Life History of Fungi and Schizomycetes.

The DAVY MEDAL to J. H. VAN 'T HOFF and J. A. LE BEL, in recognition of their Introduction of the Theory of Asymmetric Carbon, and its Use in Explaining the Constitution of Optically Active Carbon Compounds.

The Bakerian Lecture, "The Rate of Explosion in Gases," was delivered by Professor HAROLD B. DIXON, F.R.S.

The Croonian Lecture, "The Position of Pathology among Biological Studies," was delivered by Professor RUDOLF VIRCHOW, For.Mem.R.S.

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PHILOSOPHICAL TRANSACTIONS.

I. *On the Organization of the Fossil Plants of the Coal-Measures.*—Part XIX.

By W. C. Williamson, *LL.D.*, *F.R.S.*, *Professor of Botany in the Owens College, Manchester.*

Received January 18,—Read February 25, 1892.

[Plates 1–9.]

In the year 1832 the late Rev. Wm. Vernon Harcourt obtained an important fragment of a Lepidodendroid branch from a colliery at Hesley Heath, near Rothbury, in Northumberland. It was the first example seen of such a *Lepidodendron* in which much of the external organization was preserved, hence it naturally excited great interest. Probably no other fossil has ever obtained a wider notoriety. The specimen was first figured and described by Witham, of Lartington, then by the authors of the 'Fossil Flora of Great Britain,' and finally by the late Adolphe Brongniart. Witham gave to the specimen the name of *Lepidodendron Harcourtii*, after its discoverer, which name it has ever since borne; but his accompanying description was full of errors. Lindley and Hutton were not much more successful in their subsequent attempts to interpret the specimen. It was otherwise when Brongniart received a section of the fragment from Hutton, which he submitted to a very elaborate investigation. The specimen was not a perfect one. The outer cortex and leaves were wholly wanting; but the rest of its organization enabled Brongniart to base upon it the construction of a diagrammatic figure of the plant when living; this he believed would prove to be typical of that of the entire Lepidodendroid family. His pre-eminent position as a palæobotanist caused his views to be universally accepted. Brongniart's typical *Lepidodendron* contained in its interior a single vascular cylinder, enclosing a medulla, from the exterior of which cylinder the leaf-traces received their vascular elements. Later in life two fragments belonging to different plants were obtained by him, in each of which there existed the central cylinder seen in *Lepidodendron Harcourtii;* but in both cases this cylinder, which he had designated *étui médullaire,* or equivalent of the protoxylem or medullary sheaf of recent exogenous stems, was surrounded by a secondary zone of wood, developed exogenously through the instrumentality of a cambium layer. BRONGNIART was unfortunately biassed by the fact that no such secondary growth existed amongst living Cryptogams—to which group he correctly determined the *Lepidodendra* to belong. The existence of a secondary, exogenously-developed, vascular zone was a clear proof in his eyes that his new plants could not be Cryptogams; hence he referred them to the family of Gymnosperms, and connected them with the well-known Carboniferous plants called *Sigillariæ.*

The conclusions thus arrived at by the great French palæontologist were almost universally accepted at the time when I began my investigations into those subjects, some thirty years ago; I soon obtained clear proofs that many of the Carboniferous Cryptogams, unlike their living representatives, were provided with a secondary, exogenously-developed, vascular zone. That this is the case with most of BRONGNIART'S *Lepidodendra* is now an almost universally accepted fact. But these plants vary in a very remarkable manner as to the stage of growth at which this secondary development makes its appearance. In some, like the *L. selaginoides,* it exists in very young twigs. In others, like the Arran plant (*L. Wunschianum,* WILL.), the branches have to attain to very large, even arborescent, dimensions, before the smallest trace of such a growth is discoverable. The *L. Harcourtii* is one of those in which no exogenous zone has yet been observed; but the history of the Arran plant teaches us to be cautious ere we conclude that it never develops such a zone of secondary xylem. The largest branch of *L. Harcourtii* yet met with is 3½ inches in diameter, apart from its leaves. I have specimens of the Arran plant of yet larger size, equally devoid of all traces of secondary xylem; but when we come to stems of the latter plant 2 feet in diameter, we find in them the most magnificent examples of a secondary zone of wood that I have yet met with. This fact has only become known to us through a rare and fortunate accident. We find in our Coal-Measures very many, even large, Lepidodendroid and Sigillarian Trees, but unfortunately these are all mere casts of the outer surface of the cortex; each interior being only a mass of inorganic clay or sand. Hence we know nothing of what the internal organization of these arborescent forms was. But the Arran stems have been preserved for us under very different conditions. They have been imbedded, not in sand and mud like those ordinarily met with, but in volcanic ash. Their central vascular axes, with their contained medullæ, are as perfect as they were in the living plants. Not only so, but much of their cortex is equally well preserved. But for this happy and unique circumstance, we should have been entirely ignorant of the fact that a *Lepidodendron* might attain to a considerable magnitude without any trace of a secondary vascular zone making its appearance in its stem, and yet, ere it attained to its ultimate dimensions of a noble forest tree, it contained such a zone. Having, however, learnt this indisputable truth, we must admit that, though no branch of *L. Harcourtii* has yet been found possessing a secondary xylem, it would be presumptuous to deny the possibility that, if we could discover its matured stems, as we have done those of the Arran trees, corresponding results would follow. This conclusion becomes the more probable when we remember how very few there are, even of the smaller *Lepidodendra,* which have not developed a secondary xylem. The only exceptional cases that I am acquainted with are two or three of which we only know the young twigs.

I had been working at my subject for many years before I obtained a specimen of the true *L. Harcourtii.* I found some very young branches of a *Lepidodendron* which I thought might represent an early state of BRONGNIART'S plant. I had long been anxious to see HARCOURT'S original specimen, for which I searched in vain the museums of York and Newcastle ; I at length succeeded in discovering it in the former place. The authorities of the museum kindly allowed me to make a section from it ; and thus provided with an indisputable type and specimen, I had ho difficulty in concluding that no one of the plants which I had studied and described in my Memoirs was a true *L. Harcourtii.* Additional examples of the plant from the Lancashire and Yorkshire deposits were soon afterwards added to my Cabinet. Thus armed, I wrote a note to the Royal Society,* in which I pointed out some of the most conspicuous characteristics of the type, and gave to the other form which I had confounded with it the name of *L. fuliginosum.*

Being now in possession of a number of additional sections of this classic plant, I was in a position to add much to previous accounts of it. Some of the specimens being much smaller and younger, whilst others are larger and older, than those in the hands of my predecessors in the study, I am able to fill up numerous lacunæ in our knowledge of the species.† In most of these examples the outermost cortical tissues and their remarkable foliar appendages are in a perfect state of preservation. For these latter valuable additions to my Cabinets I am once more indebted to my esteemed auxiliary, Mr. LOMAX, of Radcliffe, who, after finding the specimens at Dulesgate, kindly cut them into numerous sections in such directions as seemed to me most likely to reveal the entire structure of the plant.

Plate 1, fig. 1, represents a transverse section of the smallest branch I have hitherto seen (C. N. 1596 A.).* The diameter, including its leaves, is ·75 of an inch. Its medulla, *a*, is about ·06, and the vascular cylinder *b*, surrounding the medulla, is ·15.†

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* 'Proceedings,' vol. 42, 1887.

† Three sections from different specimens of the plant have recently been investigated with great minuteness of detail by my friends Professor BERTRAND, of Lille, and M. HOVELACQUE. The results obtained by them are recorded in a Memoir by M. BERTRAND, published in the 'Travaux et Mémoires des Facultés de Lille,' entitled "Remarques sur le *Lepidodendron Harcourtii* de WITHAM," 1891. Though unable to accept all the conclusions arrived at by my colleagues, they have called my attention to several important points in the minuter details of the organization of the plant. Several of those points had already been detected by me, the figures of them drawn, and the descriptions written before I had received from Professor BERTRAND, or seen, a copy of his valuable Memoir. Unfortunately, the three sections obtained by my friends were equally imperfect with those of HARCOURT and WITHAM in having lost all traces of their outer cortex and its appendages.

On two previous occasions‡ I have pointed out that the cells of the medullæ of some *Lepidodendra* appear to have occasionally assumed an extremely active meristemic condition. These examples I now know belong to *L. Harcourtii.* The peripheral cells of fig. 1 are somewhat larger than the more central ones; and many of both have also undergone secondary meristemic subdivisions. Hence whatever may be its physiological significance, the not unfrequent recurrence of such an active meristemic condition of the medullary cells of *L. Harcourtii* is a fact that must be accepted. Is it possible to accept this truth without admitting the correlate one that a medulla, the cells of which were from time to time so extensively multiplied in number, must simultaneously have undergone a corresponding increase of its diameter, and that such an enlargement would inevitably involve a similar increase in the diameter of its investing primary tracheal cylinder? Accurate measurements of these central organs at various stages of the plant's growth became important in their bearing upon this question. The radial thickness of the primary cylinder of fig. 1 from its medullary to its cortical border averages about ·02, and the number of tracheæ counted radially between these borders, including the small peripheral ones, does not exceed from three to seven.

In vertical sections the cells of the medulla are constantly arranged in vertical lines, alike in young and older branches. They correspond in this respect with the similar organs of ferns to which De Bary so unhesitatingly applied the name of a medulla.

Professor Bertrand, of Lille, has recently described the details of the periphery of the primary tracheal cylinder, to which he gives the name of Corona. Though I am unable to accept all the detailed conclusions at which he has arrived, it must be

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* I have more recently obtained a yet smaller example, the diameter of which, including its leaves, is only ·55; that of its medulla is ·02, and of its primary tracheal cylinder ·055.

† It is extremely desirable that we should endeavour to adopt some common nomenclature for the characteristic organs of these plants. M. Brongniart applied to the vascular cylinder just referred to the name of "Etui Médullaire." In the recent translation of Solms Laubach's 'Fossil Botany,' the same cylinder, including what I regard as its enclosed medulla, is designated the *Central Xylem Strand.* We may approximate to a common terminology if we adopt this nomenclature for the central axis. We have the authority of the late Professor De Bary for designating its central parenchyma a *Medulla,* may recognise its investing vascular tube as the *Primary Tracheal*[a] *Cylinder*, and term the exogenous structure which is so often developed yet more externally, as the *Secondary Xylem Strand.* At all events this is the nomenclature that I shall henceforth apply to these several structures. The divisions of the cortex require further consideration.

‡ Memoir XVI., Plate 5, fig. 26A, 'Phil. Trans.,' 1889, and Memoir XII., Plate 33, fig. 20, 'Phil. Trans.,' part 2, 1883.

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[a] Throughout this Memoir I employ the term tracheæ in the comprehensive sense suggested by Professor De Bary, in his 'Comparative Anatomy of the Phanerogamous Ferns;' see English Translation, p. 155.

admitted that he has done good service in directing attention to the careful study of this Corona. In his figure of the structure in question,* BRONGNIART represents it as consisting of a peripheral line of festooned loops, each one of which encloses the transverse section of the tracheæ of a leaf-trace. Each of these "festons," as he calls them, appears as if composed of small tracheæ, like those occupying the entire periphery of the primary tracheal cylinder. But none of my numerous sections, including one which, like BRONGNIART'S, is from HARCOURT'S original specimen, correspond in this respect with BRONGNIART'S figure. As will be seen shortly, the true structure of this part of the primary tracheal cylinder is accurately represented in my Plate 2, fig. 5: which figure is taken, not from BRONGNIART'S original, but from another section in my Cabinet (C. N. 381) identical in every feature with that studied by BRONGNIART, though in a much finer state of preservation.† In my figure we see transverse sections of a number of vascular projections, *c*, of somewhat varied forms, alternating with many small crescentic bays, not loops, in each one of which is located the transverse section, *c*, of a leaf-trace.‡ But in the young specimens now under consideration these peculiar projections are scarcely visible. Their condition is represented in Plate 3, fig. 6, which is a faithful transcript of a part of one of these cylinders from the section in my Cabinet, 380*a*. Here we find that the already liberated leaf-trace bundles, *c'*, of fig. 5, are much more prominent objects than the projections, *c*, of the same figure.§

Before tracing the further course of these foliar bundles we must consider the condition of the cortex in these young branches. One special fact connected with an individual bundle of fig. 1 will be referred to later on.

Immediately investing, and in contact with, the periphery of the primary tracheal cylinder, we have clear evidence of an extremely delicate thin-walled parenchymatous tissue, which will be again considered on describing some vertical sections of these young twigs. External to this delicate zone we have now a vacant area, *c*, from which nearly every trace of structure has disappeared. Here and there are indications that it was occupied by an outward extension of the delicate parenchyma already described; this merged gradually into the innermost portion of the next more external cortical zone, *d*. The breadth of this vacant area is about ·1.

In his restoration of *L. Harcourtii*, M. BRONGNIART indicated that the boundary line between the cortex that once occupied the space *c*, and the well preserved tissue *d*, *d'*, was a sharply defined one. This, however, is certainly not so. The details of the structure of *d* will be best understood when we examine longitudinal sections of it. This zone appears in fig. 1 as composed of cells averaging about ·02 in diameter. They are mainly characterised by variations in the thickness of their cell-walls. In the innermost ones, *d*, the walls are extremely thin and colourless, but these cells pass very regularly into a thick walled series, *d'*, of a much darker brown tint. The diameter of this zone is about ·5. It is invested by a very similar zone of about the same thickness, but in which the cells are in a more disorganized state, yet the latter is a mere extension of the former one.

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* 'Histoire des Végétaux Fossiles,' vol. 2, p. 20, fig. 6B.

† I find an equally accurate figure in BERTRAND'S Memoir, 'Remarques sur le *Lepidodendron Harcourtii* de WITHAM,' Plate 1, fig. 5.

‡ Messrs. HOVELACQUE and BERTRAND alike refer to these projections, singly and in their combined forms, under the names of "*poles*" and "*pointements*," whilst the section, *c'*, of the leaf-traces, they designate "*pièces sortantes*."

§ This circumstance seems to me to suggest that the "*pointements*" of M. BERTRAND are of much less importance to the development and separation of the leaf-trace bundle than from his Memoir he appears to regard as probable.

Externally to the preceding layers is a thin zone of radially arranged elements, small portions of which were preserved at some peripheral points of Harcourt's specimens, and which were noticed, though misunderstood, alike by Witham, Lindley and Hutton, and Brongniart. Very little was known about this curious zone until I published Part II. of my series of Memoirs in the 'Phil. Trans.,' when I called attention to its existence under the name of the *prosenchymatous layer* of the cortex of my *L. selaginoides.* In fig. 5 of Brongniart's Plate 20, already referred to, he copied from the 'Fossil Flora of Great Britain,' a figure which its authors represented to be a longitudinal section through the tissue in question. This it certainly was not. In my Memoir just referred to I pointed out that in its developed condition this tissue was composed of cells which were "elongated vertically and, at last, pass rapidly into the almost vascular form of prosenchyma" (*loc. cit.*, p. 200, and Plate 24, fig. 1*i* and fig. 2*i*). On p. 211 of the above memoir I called attention to a copious development, in the same part of the cortex, of a similar prosenchyma (*loc. cit.*, Plate 27, fig. 29*d*); and again at p. 213 of the same publication I showed the existence of an identical structure in a Syringodendroid form of *Sigillaria*, belonging "to the group of *S. Saullii*, *Schlothemii*, and *Scutellata*."

At a much later period (1881), in my Part XI., I not only again directed attention to the existence of this cortical prosenchymatous zone, but I now announced my observation that its radially arranged cells (Plate 51, fig. 2*f*) were generated at an undulating circular line which constituted the external border of the zone, the whole being primarily derived from a thin cellular layer of the cortex interposed between the leaf-cushions and the prosenchymatous zone. But my most complete notice of what appears to me to be the true history of the development of this tissue was only announced in 1887 in my Memoir on *Stigmaria ficoides*, published by the Palæontographical Society (pp. 18–22, figs. 22, 23, 24, and 24A). In this publication I demonstrated the existence of what I ventured to call a *bark-cambium* between the outermost cortex and its prosenchymatous zone, and through the meristemic actions of which additions were constantly made to the exterior of that zone, throughout the greater portion of the life of the plant; it being further evident that such copious thickenings of the cortex equally affected the aerial stems, the branches, and the Stigmarian roots. One fact more connected with this prosenchymatous zone is seen in the specimen represented by fig. 1. Its first development in young twigs does not advance simultaneously throughout the entire circle of the cortex. In the example fig. 1*f* there is an arc, the chord of which is about ·5 of an inch in length, in which the zone has not yet made its appearance, whilst on the opposite side of the circle each radial line of the prosenchymatous cells contains fully a dozen of them. Outside this zone we have the outermost cortical zone, which we shall understand best by referring to my enlarged figures of some of these structures as seen in longitudinal sections.

In fig. 2 we have a segment of the cortex and leaves of fig. 1 enlarged eight diameters. Of the innermost cortex of the twig we here see no trace; but at *d* we find the more delicate cells of the inner half of the middle cortex. The innermost margin of this zone consists of oval cells arranged somewhat concentrically, their shorter axes being their radial ones. More externally, *d'*, they became more irregularly circular. In fig. 4 we have four radial lines belonging to the prosenchymatous zone, *e*, with the outermost cells of the middle cortex at *d*, and those of the outermost cortex at *f*. The breadth of this zone is about ·02; fig. 4 is enlarged about fifty diameters. The leaves must be considered separately.

Of the longitudinal aspects of the medulla and its investing primary tracheal cylinder there is little to be remarked beyond what we find common to most of the other *Lepidodendra*, viz., the barred structure, and the large size of the more internal tracheids, contrasted with the small diameters of the peripheral ones. I discover, also, in all these young twigs of *L. Harcourtii*, the condition previously noticed in *L. Wunschianum* and in *L. Mundum.** The transverse bars of the tracheids are connected by innumerable very delicate vertical threads. I find no trace of these in vertical sections of my older branches of *L. Harcourtii*, where such threads are conspicuous in my Arran plant.

One other feature occurs here and there at the periphery of the primary tracheal cylinder, viz., the existence of vertical lines of a few barred cells. Two illustrations of these from the Cabinet specimen 1596D are given in Plate 1, figs. 2*a* and 2*b*. The mean vertical length of each cell is about ·025.

Vertical sections of the middle and other external structures of the cortex are shown in figs. 9 and 9A on Plate 2, enlarged four diameters, and still more definitely in fig. 10, which is enlarged fifteen times. We here see the delicate, thin-walled cells of the middle cortex *d*, passing into the more robust ones at *d'*. The elongated tubes of the prosenchymatous zone are conspicuous at *e*, whilst at *f* the thin layer of cells representing the outermost cortical parenchyma interposes between the zone *e* and the bases of the leaves *g*. In the vertical sections, as in the transverse ones, I not unfrequently find the zone *f* distinctly developed on one side, whilst little or no trace of it is visible in the cortex on the opposite side of the same section.

Fig. 3, Plate 1, represents a transverse section, natural size, of a very much larger stem from Airdrie in Scotland. Its mean diameter within the periphery of its prosenchymatous zone, the most definite boundary line for exact measurements, is about three inches. This is the largest stem or branch of *L. Harcourtii* that I have hitherto seen or heard of. A lateral view of the entire specimen from which the section fig. 3 was cut is given in Plate 5, fig. 7. Its medulla *a* has a diameter of ·3, while that of fig. 1 is only ·06. The primary tracheal cylinder *b* has, in like manner, expanded from ·15 to ·5 of an inch. The mean radial thickness of this cylinder averages ·08, whilst that of fig. 1 was about ·02, and the approximate number of tracheæ that can be counted radially between the medullary and cortical margins of fig. 3 is twelve, contrasted with the five or six of fig. 1.* The arrangement of the peripheral tracheæ of this cylinder corresponds in all essential features with those of fig. 5, Plate 2. We find the leaf-traces, at c', as in that figure, and the varied intervening prominences as at *e*; but all these peripheral features are rendered somewhat obscure by their being projected into a zone of dark-coloured, extremely delicate parenchyma, which has a radial thickness of about ·02. This, I presume, must be regarded as a phloem zone composed of soft bast, and identical with the "Liber" of M. BERTRAND. I cannot detect in it any trace of that author's "gaine protectrice," the equivalent of the bundle-sheath of English and German authors.

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* See Memoir XVI., Plate 5, fig. 14*a*, 'Phil. Trans.,' vol. 180, 1889.

We now come to the zone *c*, from which all cellular structure has so frequently disappeared; but here, especially in the part to the right of the figure, between c' and c'', as well as at various other points within the area originally occupied by the inner cortex, we have definite evidence as to the structure of that tissue. It clearly consisted of an extremely delicate and, apparently, uniform parenchyma, which gradually passed, as I have already suggested, into that composing the innermost portion of the middle bark. With the exception of the latter fact, these conditions are in accordance with the views of BRONGNIART as shown at D, D, of his fig. 1, Plate 21.

The structure of the middle cortex, *d*, varies somewhat from that represented in my Plate 2, fig. 10, though there is less difference in the thickness of the cell-walls of the inner and outer cells, and there is a strong disposition in many of the former to arrange themselves in radial lines, whatever this may signify. Turning to the prosenchymatous zone, *e*, we see that it has undergone a large increase of radial thickness. What, to the naked eye, seems to represent its sharply-defined peripheral boundary really runs nearly through its centre. Outside that line we find a further extension of its radial rows of the square transverse sections of its prosenchymatous cells, giving a thickness to the entire zone of ·2. A conspicuous feature of this zone is its undulating course. At numerous points, as at e', e', it is projected outwards at a very acute angle, thus giving to its entire outline a crenulated aspect, the crenulations being directed inwards; and we further learn that at each of the projecting angles a leaf-trace has emerged, to reach a leaf. Why this leaf-trace cannot be seen in every one of these emergent points is easily understood by a fact of some importance to our comprehension of conditions observable in many of those arborescent stems which are imbedded in shales and sandstones, but retain little or no portion of their organized structure.

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* These details may appear uninteresting, if not pedantic; but they have a very important bearing upon the problem of the growth and development of these branches.

Turning to Plate 5, fig. 7, we have a representation of one side of my stem (C. N. 380 X) from which the original of fig. 2 was cut. The face x, x corresponds to the peripheral arc of fig. 3 indicated by the same letters. That surfaces similar to that here exposed, having spiral series of vertically elongated conical protuberances, represent semi-decorticated *Lepidodendron* stems and branches has long been understood. Equally obvious was the probability that leaf-traces issued through each of these fusiform projections. But we were wholly devoid of information as to which special cortical zone these partially decorticated specimens represented.* The specimen, fig. 7, taken in connection with Plate 1, fig. 3, conclusively settles all these questions. Externally to the prosenchymatous zone we find here at *f*, *f*, in fig. 3, the usual thin outermost cortical layer of parenchyma supporting the leaf-cushions. Immediately within this, as at e', e', are the angular projections of the prosenchymatous zone, through several of which, as already observed, the leaf-traces can be seen emerging. The specimen demonstrates that these projecting angles are identical with the fusiform protuberances, *f*, between x and x of fig. 7; and we further learn that the surface in question represents the centre, or nearly so, of the prosenchymatous zone.

The Leaves.—No one has hitherto described any trace of these organs of *L. Harcourtii.* Now, however, we have them in abundance. But before examining the details of their structure, it may be well to follow the course of the leaf-traces from the points at which they leave the primary tracheal cylinder to those at which they enter the leaf-cushions.

During the last two years much attention has been given to the structure of Lepidodendroid leaves by Professor BERTRAND and by M. HOVELACQUE. In several of my previous Memoirs I have figured some conspicuous objects (*e.g.*, Memoir XI., Plate 47, g', g', g') which I mistook for large leaf-traces; but at p. 285 of the same Memoir I noted that "in each of the three leaves of fig. 1 in which this bundle appears there are peculiar condensations of the cellular tissue of the leaf." These observations are accurate, but, from the lack of more numerous sections other than transverse ones, I failed to discover the true contours of these organs. This, however, my two friends above named have done. The organ in question is evidently common to many of the *Lepidodendra*, though its significance has been overlooked by me until the two observers mentioned called my attention to it. At the same time I cannot accept the name they have given to the structure. They call it the *Ligule.* I cannot, however, recognise any homologous relationship between the membranous ligule of the living *Selaginellæ* and *Isoetes* and the peculiar organ of our fossil ones. Many features about the latter suggest strongly that it may have been a glandular structure; hence I shall distinguish it by the name of the adenoid organ of the leaf.

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* I may call attention, in passing, to a very characteristic stem of this type connected with the fine *Stigmaria* recently discovered at Osnaburg, and now in the Berlin Geological Museum. See "Der im Lichthof der Königl. geologischen Landesanstalt und Bergakademie aufgestellte Baumstumpf mit Wurzeln aus dem Carbon des Piesberges," von HERRN H. POTONIÉ, in Berlin, Plates 21 and 22 Separatabdruck aus dem 'Jahrbuch der Königl. Preuss. Geologischen Landesanstalt für 1889.'

Another organ is referred to by the same observers under the name of *parichnos*, assigned to it by M. BERTRAND. I had already worked out this organ, and prepared my figures and descriptions of it as they appear in the succeeding pages, when I received the Memoirs of MM. BERTRAND and HOVELACQUE, in which they speak of it. M. HOVELACQUE is inclined to regard it as a glandular structure. M. BERTRAND objects to this conclusion, and has adopted a name which he thinks sufficiently indicates his objection. Since I agree with M. BERTRAND on this point, I shall accept and employ his name of *parichnos*.

I have already observed that the arrangements of the small tracheæ at the periphery of the primary tracheal cylinder of my young twigs, illustrated by my fig. 6, Plate 3, are much less complicated than in the larger branches described by M. BERTRAND. This simpler condition is still more conspicuous in my yet younger, more recently-acquired section (C. N. 1596 G.), where the primary tracheal cylinder is closely invested by a zone of delicate, well-preserved parenchyma, ·01 in diameter. In this specimen the "points" of M. BERTRAND are less prominent even than in my other young branches, whilst the leaf-trace bundles are large and conspicuous. It is difficult to trace these bundles far down the exterior of the cylinder in longitudinal sections. They become inextricably intermingled with the numerous small tracheæ as well as with the cells, some spiral, others not, that often occupy the line of junction of the common bundles and the innermost cortex, or *couche libérienne* of my French friends. (See C. N. 3892). Where the leaf-trace first becomes fairly detached from the periphery of the primary tracheal cylinder, it consists solely of a number of very small tracheæ. Scarcely any portions of these are preserved, in the young specimens, in the vacant area between the neighbourhood of the cylinder and the inner border of the middle bark. But we not only find them at the innermost margin of the latter (as in figs. 9, 9A, and 10, at *c*, *c*), but they here present the double form characteristic of *L. Harcourtii*, having the inner and upper part composed of tracheæ, and a lower and outer portion consisting of an admixture of hard and soft bast—obviously the xylem and phloem of modern writers. A bundle in this condition is seen, intersected a little obliquely, in fig. 8, and another, cut across yet more obliquely, in fig. 11. In the former figure (C. N. 1596) we have the xylem on the left hand, *a*, and the phloem on the right hand at *b*. In fig. 11 we have the same arrangement at *a* and *b*. These arrangements are reversed in Plate 1, fig. 12, where *a* is the cluster of the tracheæ of the xylem, and *b* the hard bast of the phloem. In fig. 8 only the xylem and hard bast are preserved within the small circular area, *c*, from which all more delicate structures have disappeared. In fig. 11, which section is rather more oblique, we find, in addition to the leaf-trace, a number of very delicate cells, elongated longitudinally, some of which doubtless represent the soft bast. In some transverse sections we find the area *c′* of figs. 8 and 11 filled with similar delicate cells investing the entire bundle. These cells suggest the idea of a concentric bundle, but on the whole I incline to the belief that they are really collateral.

In my larger branches, further points may be noted. In Plate 1, fig. 3, we find sections of a considerable number of leaf-traces, *c''*, scattered irregularly over the vacant area *c*. Each of these traces is surrounded by a zone of extremely delicate parenchyma, within which we find, in many cases, the phloem and xylem distinctly preserved in their normal positions. On reaching the middle cortex, *d*, these bundles, *c*, become extremely conspicuous, each of them occupying a circular or oval area, about ·1 inch diameter. On this large specimen we can readily trace the symmetrical diagonal curves, along which the sections of these leaf-traces are arranged; curves which correspond to the diagonal arrangements of the leaves at the exterior of the cortex. In each of these curves I usually find three leaf-traces, though, occasionally, a fourth can be detected at the periphery of the cortex. These diagonal curves start from the inner margin of the middle bark, and bend away in a segment of a circle towards the periphery of the cortex, the concavity of each curve pointing towards the centre of the branch. I find that the curves which bend outwards from left to right are twenty-four in number, whilst of those curving from right to left there appear but sixteen. On reaching the prosenchymatous zone of the cortex we find a new element associated with the leaf-trace. A tangential section of this zone of the cortex, intersecting one of these leaf-traces, is represented in fig. 13 (C. N. 380*k*), × 37. The imperfectly-preserved vascular bundle is seen at *c'*, whilst immediately above it we have, at *g*, a transverse section of the organ to which M. BERTRAND has given the name of "parichnos." No student of Carboniferous vegetation is ignorant of the fact that near the centre of each leaf-scale, left after the fall of the leaf of a *Lepidodendron* or *Sigillaria*, there are three small distinct marks. BRONGNIART believed all three to represent a similar number of leaf-traces. We have long known, however, that this was not the case. The central one alone is of that character, but what the other two were has long been unknown. The Memoir of M. BERTRAND throws some light upon them and gives them a name, but long before that Memoir was published I had obtained two magnificent series of sections of these objects illustrating their entire morphology. On making tangential sections like fig. 13, we find in *L. Harcourtii* a *rounded* cluster of cells enclosed in what resembles a more or less distinct sheath *resting upon* the upper surface of the vascular bundle. On a later page, similar, though modified, conditions in the corresponding parts of a Ulodendroid branch of a *Lepidophloios* will be described.

We may pause here for a moment to consider the external forms of the leaves of *L. Harcourtii*, as seen in transverse, radial, and tangential sections. Their outlines in transverse sections of the branches are seen in Plate 1, figs. 1 and 2; in longitudinal ones, Plate 2, figs. 9 and 9A; and in a tangential section, Plate 2, fig. 14. Further enlarged views, and more detailed organization, are represented in Plate 3. Of course, the forms of these leaves necessarily vary according to the planes, horizontal or vertical, in which they are intersected, but all the variations show that these organs were extremely short and more or less quadrate in form, but having a somewhat prominent apex. Their fundamental tissue is parenchymatous, the cells becoming smaller, and with thicker walls, as they approach the epidermal surfaces, and in the immediate vicinity of the special organs seen in their interior. Fig. 14 shows their bases to be almost as quadrangular as those of a *Favularia;* but Plate 3, fig. 15, represents some of these leaves as they appear at part of the exterior of the specimen, Plate 5, fig. 7. I have ground these down in an unequal degree, dipping deepest into the specimen to the right of the figure where the sections are becoming more rhomboidal than in Plate 2, fig. 14. They are also much further apart than in the latter figure. On the left, I have chiefly brought their widely-separated tips into view. Here the small sections are almost triangular.

To master the details of their internal organization I have been compelled to obtain a very large number of sections of these leaves, since a complete knowledge of their structure could only be derived from the study of many such sections, made in a variety of planes. The chief special organs in their interiors consist of the leaf-trace, the parichnos, and the adenoid organs.

Plate 3, fig. 16, represents part of a leaf from the transverse section of a branch (C. N. 380*b*), × 27, in which the leaf-trace, *c*′, passes through the prosenchymatous zone, *e*, and terminates at *c*″ in a fan-shaped arrangement of prosenchymatous cells, amongst which two or three barred ones can be detected.

Plate 3, fig. 17, represents a similar section to fig. 16, only the leaf is cut through at a slightly different horizon ; hence at *g*, *g*, we now find the single parichnos, *g*, of fig. 13, divided into two, for the organ bifurcates soon after leaving the prosenchymatous zone of the cortex. Fig. 18 represents a similar section to the two last, showing sections of the two lobes of the parichnos, *g*, *g*′, but here the end of the leaf-trace, fig. 16, *c*″, has been intersected obliquely at *c*″ ; we now find that all the elongated cells which pass upwards in the direction of the apex of the leaf-trace are barred tracheæ, whilst those which pass downwards are ordinary prosenchymatous cells, an apparent division of the two constituents of the leaf-trace.

Plate 3, fig. 19, is one of the few vertical sections in which I have been able to observe the course of the leaf-trace from the middle cortex into the leaf. At *c* the trace distinctly displays the division into phloem and xylem. In the interior of the leaf this distinction cannot be observed. This trace seems to terminate below the apex of the leaf, and immediately above a point where the margin of the leaf is more deeply lobed than usual. Close to the apex of this leaf, *k*, we discover the organ to which I have given the name of adenoid, but which my French friends designate the ligule. We see it again at *h*, *h*, in a similar position, in the vertical sections through two leaves, figs. 20 and 21. We shall find this organ much more perfectly developed, though in a different position, when we examine the leaves of

Lomatophloios. The fact to be noted here is that the peripheral termination of this organ is at the prominent apex of each leaf.

I should next proceed to examine what I am convinced represents a series of Halonial states of *L. Harcourtii*, but before doing so it becomes necessary to submit to a careful enquiry what we must, in future, imply by the terms *Halonia* and *Ulodendron*, and especially whether we can any longer use these terms as generic names, or whether we must simply employ them as adjectives to indicate either a preparation for, or the actual attainment, of the condition of special fruit-bearing branches of any or all of the Lepidodendroid and Sigillarian plants.

I must first insist upon the recognition of some more definite characteristics distinguishing *Halonia* from *Ulodendron* than we yet possess. In Part II. of my Memoirs ('Phil. Trans.,' 1872), I introduced a long note on the close relations which then appeared to me to subsist between *Halonia* and *Ulodendron*. After 20 years of further study of the question, I find very little (and that little only applies to some minor points advanced hypothetically) that I am prepared to withdraw.

In his 'Tableau des Genres de Végétaux Fossiles' (1849), BRONGNIART, speaking of *Ulodendron*, says: "Ce genre ne me paraît fondé que sur un état particulier de certains *Lepidodendron*, dans lesquels il se développe sur les tiges volumineuses des tubercules coniques ou hémisphériques." He goes on to say: "Ces sortes de mamelons orbiculaires sont disposés en série longitudinale sur les deux côtés opposés de la tige à des intervalles assez rapprochés" (*loc. cit.*, p. 42).

On the next page he briefly describes the genus *Halonia*, respecting which he remarks that whilst Lepidodendroid in its general features, "la tige présente en outre de gros tubercules coniques *disposés en quinconce*, et sur lesquels s'étend uniformément l'écorce générale et les feuilles qu'elle supportait" (*loc. cit.*, p. 225).

Since these definitions were penned we have learnt much about *Halonia* and *Ulodendron*. In Memoir II. (*loc. cit.*, p. 225) I expressed my strong conviction that the tubercles, alike of *Ulodendron* and of *Halonia*, represent short abortive branches destined to support strobiloid forms of fructification. The accuracy of this conclusion was set at rest for ever when Professor D'ARCY THOMPSON discovered and described one of the forms of the so-called *Ulodendron minus*, with the strobilus *in situ*, attached to its Ulodendroid scar. That the *Haloniæ* were young terminal branches, and not roots, as many, including BRONGNIART himself, were inclined to believe, was in like manner set at rest, first by the final demonstration that the *Stigmariæ* were the true roots of the *Lepidodendra*, and, secondly, by my publication of the figure of the grand specimen in the museum of the Leeds Philosophical Society,* which settled, beyond all possibility of question, the fact that *Haloniæ* were the terminal divisions of Lepidodendroid branches. Starting from this foundation, I shall proceed to examine such facts as we are now acquainted with bearing upon this question.

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* Memoir XII., Plate 34, 1883.

In the first place BRONGNIART's division of *Ulodendra* and *Haloniæ* into two groups, in the former of which the tubercles are in the centre of large flattened scars arranged in *two* vertical series on opposite sides of the stem, whilst in the latter we have *numerous* rows of similar tubercles arranged quincunctially, can no longer be accepted.

Plate 6, fig. 22, represents a small branch in my collection (C. N. 649 A) of its natural size, with the *tubercles* arranged as in *Ulodendron,* three on one side, *c, c, c,* whilst two on the opposite one occupy the centres of the two intervals *c, c.* The specimen is semi-decorticated, and in a condition identical with that of fig. 23 and the front portion of fig. 24. On comparing these three specimens it will at once be seen that the tips of their respective tubercles are in precisely the same condition. They all alike represent areas which reached the surface of the cortex, and through which *special* bundles of vessels passed into the slender axis of the strobilus which each tubercle once supported. Fig. 22 is obviously the youngest of these three branches, 24 being the next, and 23, which is reduced from the size of the original by one-third, has clearly grown enormously since it was a young terminal fructiferous branch. Figs. 23 and 24 obviously belong to the form known as *Halonia regularis,* and each of them has enlarged considerably beyond their normal diameter when they first began to develop as small lateral, arrested, fruit-bearing branches, of which the tubercles are the remaining indications. In the Owens College Museum, to which the specimens, figs. 23 and 24, belong, we have other much more slender branches of the same type, some of which are not more than ·5 in diameter.*

Before leaving the above three specimens, I would again call attention to the absolute identity in the form and aspects of their several tubercles as indicated by the letters *c, c.* In each case we have a small fractured circular area which once sustained some deciduous appendage. Had the prolongation beyond the broken circular area not been some deciduous organ, but merely abbreviated lateral branches, it would have been impossible for these tubercles to have retained such an absolute regularity of elevation, size, and form as they all present. It is obvious that each shoot was originally prolonged into something that is no longer preserved *in situ.* We are forced to the conclusion that the missing appendages must have been strobiloid reproductive organs. Turning to Plate 6, fig. 25A, we meet with further characters of interest. I am indebted for this important and beautiful specimen to my friend T. W. DAVIS, ESQ., F.G.S., of Chevinedge, near Halifax, who obtained it from a colliery in the neighbourhood of Wakefield. The specimen represents the exterior surface of the cortex, the leaf-cushions of which are beautifully preserved. Its striking feature consists in its three contiguous vertical columns of true Ulodendroid scars arranged in the so-called quincunctial manner characteristic of the tubercles of *Halonia regularis.* BRONGNIART describes this arrangement as quincunctial, but it is as easy to demonstrate that the circle of tubercles, of which each one is in turn a centre, consists of six, as of five. This is also the case with fig. 25A, in which the scars of each vertical series alternate, and are in close contact with each other within each circle. We have the usual broad Ulodendroid area which was merely compressed by, but not organically united with the deciduous appendage. The true point of organic union is very distinct in most of the circles, but especially so in those indicated by the letter *c*. On comparing these central points with the middle one, *c* of fig. 22, as well as with those similarly indicated in figs. 23 and 24, no doubt can be admitted to exist as to their being homologous. But this specimen suggests some further enquiries. On Plate 8, fig. 2, of his classic work on the 'Flora of the Primæval World,' STERNBERG represented a fragment of a Lepidodendroid bark, to which he gave the name of *Lepidophloios laricinum.* This figure is indefinite, in addition to being, in my conviction, turned upside down. Still, later, CORDA figured and described under the new name of *Lomatophloios*, a somewhat similar plant, and GÖPPERT a third, to which he gave the generic name of *Pachyphlœus.* Referring to these three plants, in 1849,* BRONGNIART says: "Ces trois genres me paraissent des espèces différentes d'un seul et même genre, auquel je laisse le nom donné en premier par M. DE STERNBERG," a determination with which I heartily agree, and could wish to see it adopted at the present day. Amongst other definitions of the genus *Lepidophloios,* BRONGNIART defines the cortex as "couverte d'écailles formées par les protubérances basilaires des feuilles, elles sont à peu près rhomboïdales, à grand diamètre transversal, terminées à leur angle *supérieur* par une cicatrice d'insertion des feuilles également rhomboïdale."

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* The specimen fig. 18 is the one originally figured by Mr. BINNEY, and part of which was refigured from BINNEY's plate by M. RENAULT, where a mere crack in the matrix was represented as a rootlet, and quoted as proving that *Halonia* had been a root like *Stigmaria.*

The above observations by STERNBERG and CORDA have led to a protracted controversy that has not yet come to an end. The opposing parties equally recognise the general form of the leaves of STERNBERG's *Lepidophloios* and CORDA's *Lomatophloios* as being identical, viz., that the transverse diameter of each rhomboidal leaf-base greatly exceeds its vertical one, and that its prolonged lateral angles are very acute, whilst its upper and lower ones are obtusely rounded; but the dispute that has arisen refers to the position of the leaf-scar, left by the fall of the deciduous leaf, upon what remains in the shape of a persistent pulvinus, or leaf-cushion. In his figure of *Lepidophloios laricinum* (Plate 2, fig. 2, of his work on the 'Flora of the Primæval World'), STERNBERG places this leaf-scar on the lower vertical angle of each leaf-cushion, the reverse of its usual position amongst the Lepidodendroid plants. At a later period, in his 'Flora der Vorwelt,' CORDA figured a plant under the name of *Lomatophloios crassicaule,* in the leaf-cushions of which he reverses this arrangement. BRONGNIART, as we have seen, unites the two genera in question with a third one, and assigns the superior position to the common group; later observers ranged themselves on opposite sides of this division; GOLDENBERG restored both the genera *Lepidophloios* and *Lomatophloios*, assigning the upper position to the former one, and the lower to the latter, a course lately followed also by RENAULT. WEISS, in my mind, far more judiciously, reverted to BRONGNIART'S plan, and reunited the two genera.

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* 'Tableau des Genres de Végétaux Fossiles,' p. 43.

But it is to be noted that most of the fragments of the plants concerned bear no characteristics enabling us to determine which is the upper and which the lower end of the specimen. This is the case with STERNBERG'S original figure; hence it would appear more reasonable that, in the absence of other features distinguishing *Lepidophloios* from *Lomatophloios*, the two should, in accordance with the views of BRONGNIART and WEISS, be united under the former name, as being that first published. But a small addition to the definition of the former, already quoted, should recognise the fact that in some examples of the genus the leaf-scar may occupy the inferior position. Anyhow, such will be the plan adopted in the following pages.

These Lepidophloioid leaves are well preserved in the fructigerous branch of which fig. 25A represents the natural size. Each circular area corresponds to what was primarily a very slightly projecting deciduous branch. In the centre of each circle is the flattened mamilla, *c*, of a Halonial tubercle. The Lepidophloioid leaf-cushions are arranged also in circles surrounding each Ulodendroid area. This arrangement is exactly what would occur where any young leafy shoot sprang laterally from a more vertical primary one.

In this specimen we thus find combined the tips of the tubercles and the multiplied vertical rows of a *Halonia* with the flattened orbicular areas of a *Ulodendron*. The question arises, what is the meaning of these combinations. I think the probable answer is easily found, but in seeking it we must first turn to the two fine specimens, figs. 26A and 27A.

Fig. 26A represents a specimen from the Lancashire coalfield, now in the Museum of the Owens College. The figure is reduced to two-thirds its actual size. We have here a Lepidodendroid stem, *a*, clothed with the long leaves of the Lepidophylloid type, so different from those of *L. Harcourtii* and its allied forms.

On its right we have a very short branch, *a'*, the development of which has been arrested by the growth of the fine *Lepidostrobus*, *b*, still united to it. If this cone could have been detached, we should, I doubt not, have found at its base, deep amongst the surrounding leaves, an area, the diameter of which would be the same as that of the base of the strobilus. The pressure of the latter would necessarily check the development of the underlying leaves. But in the centre of that compressed area would be a yet smaller circle representing the point of organic union between the abortive branch and the axis of the strobilus. This latter point would, after the fall of the strobilus, correspond in all its features with what we see in the centre of each of the scars, *c*, of fig. 25A. In fig. 27A we have a different arrangement. Here the strobilus, instead of being practically sessile upon an undeveloped *lateral* branch, hangs from the extremity of a slender terminal twig, to the growth of which the presence of the reproductive organ has occasioned no apparent interruption.* I infer from the above and other similar examples that true Ulodendroid scars, whatever may be their number or arrangement, were produced by the pressure of strobili devoid of any conspicuous peduncles, and which, though really terminal upon arrested *lateral* branches, bore the aspect of being planted in a sessile manner, on the sides of ordinary ones.

In the *Haloniæ,* on the other hand, the peduncle of the strobilus, though short, projected sufficiently above the cortex to prevent the base of that strobilus from pressing so closely upon the sustaining branch as to depress or destroy any of its leaves. Of course, this result would be influenced by variations in the shape and size of the base of the strobilus. When this was fusiform and narrow, it would further facilitate the development of the Halonial type of tubercle. A conical strobilus, on the other hand, with a broadly obtuse base, would further tend to produce the Ulodendroid form. Such examples as fig. 27A carry us to the very extreme form of plants on the branches of which no traces of the detached organs of fructification remain.

It follows from the above observations that the only distinction between Halonial and Ulodendroid conditions lies, not in the number or arrangement of the fruit-scars, but in the presence or absence of a pressure disk surrounding each true fruit-scar. The flattened examples so common amongst the Carboniferous shales are in a most abnormal condition. The larger ones represent old arborescent stems from the interiors of which every trace of organic matter has disappeared; nothing remains of the original branch save a very thin film of coal, on the surface of which is impressed many of the details of leaf-scars, &c., with minute exactness; but such stems, reduced by decay to the state of thin-walled unresisting cylinders, thrown down and overlaid by masses of mud and sand, soon had all the undulations of their exteriors reduced to a more or less uniform plane.

The normal contours of such arborescent Ulodendroid forms, not altered by vertical pressure, are seen in a noble specimen in the Museum of Owens College. This stem is 7 feet 6 inches in height, and has a circumference of 3 feet at 1 foot from its upper end, of 45 inches at a lower point, and of 48 inches near its base. It has eight scars on each side, at intervals of about 11 inches between the centres of the scars; each centre being at the bottom of a deep depression, apparently produced by the outgrowth of the thick surrounding cortex, such as we find in any old tree wherever the removal of a branch in its youth has left an area uncovered by that cortex. This fine specimen was obtained from the Colliery of Messrs. MILES, SETTLE, and Co., at D'Arcey Lever, and presented by them to the College Museum. It is an example of the kind of specimen that must be studied if a true conception of these Ulodendroid forms is to be arrived at. For the specimen, fig. 27A, which I presented to the Owen's College Museum, I was indebted to CHARLES B. CRAWSHAW, Esq., of the firm of CRAWSHAW and WARBURTON, in whose "Saville" pit at Soothill, near Dewsbury, the specimen was found in a layer immediately above the Joan Coal.

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* I have lately received from SIR WILLIAM DAWSON a photograph of a fine example resembling fig. 27A, which he proposes to call *Lepidodendron Cliftonense.*

The way is now cleared for reverting to the internal structure of some of these Halonial and Ulodendroid forms, of which I fortunately possess very fine examples. In the long note in my Memoir, Part II., to which I have already called attention, I described the way in which small but complete segments of the entire primary tracheal cylinder were sometimes detached to form the vascular bundles supplying the fruiting branches, the result of which segmentation was that at the point whence this diverted segment had been removed, a gap was left in the vascular cylinder analogous to the "foliar gap" seen in ferns under somewhat similar conditions, and described by DE BARY. GRAF ZU SOLMS on p. 231 of his 'Fossil Botany,' English translation, refers to the section described in my Memoir II. He says, "I have seen the preparations in WILLIAMSON'S collections, but they have unfortunately never been figured." I now remedy this omission.

Plate 2, fig. 25, is a vertical section, enlarged five diameters, of part of a Halonial or Ulodendroid branch of *Lepidodendron fuliginosum*, which bore some distinct tubercles. We have the medulla of the main branch at *a*, enclosed within the primary tracheal cylinder at *b*. At *c* an ordinary leaf-trace is being given off from the exterior of the cylinder. But at *l* an *entire segment* of the cylinder is detached, and proceeds outwards in the same direction as the leaf-trace *c*; and through the gap thus produced in the cylinder, the medulla *a* and the innermost cortex *d* are brought into contact, the cells of the former being readily distinguishable by their size, being larger and their shapes more irregular than those of the cortex. The divergent bundle, *ll'*, consists apparently of a solid cluster of barred tracheæ without any trace of a central medulla. It is accompanied in its outward course, especially on its underside *m*, by numerous parallel lines of small cortical cells; these may possibly represent phloem elements. The radial arrangement of this tissue constitutes a very conspicuous feature of transverse sections of *L. fuliginosum*. I presume that this is the tissue to which M. BERTRAND gives the name of Liber. The above may be accepted as an example of one of ordinary methods in which these fruiting branches obtain their supplies of vascular tissue. I have previously described a slightly different way in which these fruiting branches obtain similar vascular supplies. Thus in my Memoir, Part XII., on Plate 32, figs. 21, 22, 24, and 25, and on Plate 33, fig. 23, I have represented various conditions of the Halonial branch of the Arran *L. Wunschianum*. There is no medulla in the central xylem strand in any of the *young* twigs or branches of this species. The xylem strand consists of a solid mass of tracheæ. A cluster of these tracheæ is pinched off from the exterior only of the strand which becomes moulded, on its way outwards through the cortex, into a solid cylinder like that of fig. 25 *l*.

Having thus endeavoured to sketch the general features of the fruiting branches of these Lepidodendroid plants, I must now return to *L. Harcourtii.*

In Plate 1, fig. 1, I have represented at *b′* a small segment of the primary tracheal ring, which is being detached and is carrying along with it, at its inner surface, some of the medullary cells. We have here a parallel example to what I have represented in Plate 5, figs. 1 to 6, of my Memoir, Part XVI., where a similar arc of a vascular cylinder, fig. 3, carries along with and on one side of it, a cluster of medullary cells. In fig. 3 we find this arc converted into a solid terete bundle from which all recognizable cells have disappeared. This example bears, in an important manner, upon some questions about to be considered. Had such a succession of different conditions merely been detected in an unconnected manner in several distinct but homologous bundles, even in the same plant, though the facts might have given us strong grounds for concluding that one and the same bundle could undergo similar alterations of structure in the several parts of its continuous course, we should have had no absolute proof that such changes did take place. But in the example quoted above we have positive demonstration that such changes are not only possible, but that they do actually occur. The several sections referred to above, were prepared with the utmost care and exactitude, and represent the changes undergone by the same identical bundle between its first separation from the primary tracheal cylinder to its arrival at the outermost zone of the cortex. We may therefore expect to find that a segment like fig. 1*b′* of this Memoir may undergo similar changes, and our expectation will not be disappointed.

Plate 1, fig. 26, represents a transverse section of a branch of *L. Harcourtii,* which is in the Halonial state, but in which the lateral abortive branches seem to have been more or less biserial. The primary stem *A* scarcely differs from fig. 1, the medulla *a* and its primary tracheal cylinder *b* being substantially identical in the two cases, which remark is equally applicable to the cortex and the leaves. But, in addition, we have the two lateral branches *B* and *C* springing from opposite sides of *A*, and from the difference in their degrees of growth they seem to have been given off in alternating order. Their cortical zones and foliage differ in no respect from their continuations round the central stem, but this cannot be affirmed of the central bundles *l′l* and *m′m* of the branches. In each of these the central xylem strand consists of a single cluster of tracheæ, no separation into medulla and primary tracheal cylinder having taken place; fig. 28, *a*. (I have in my cabinet a second section (C. N. 380*a*), also × 4, but which has intersected the tubercular branch *B* nearer to its apex, as is indicated by its smaller diameter. This section of *B* is represented in fig. 27). As already mentioned each of these arrested branches was clothed with the ordinary leaves of the species up to its apex. Fig. 29 is a vertical section through another of these Halonial twigs, in which *A* is the primary axis, and *B* the arrested Halonial tubercle. At *a* we have the primary xylem strand, differentiated into medulla and primary tracheal cylinder; whilst at *b* we have, separating from *A*, a large strand resembling that already represented at *l*, in Plate 2, fig. 25. This strand is further enlarged in Plate 4, fig. 29*. On examining the transverse section of a similar strand, as represented in the enlarged fig. 28, we discover that it consists of a central mass of tracheæ, *a*, within which no traces of medullary cells can be detected. This strand of tracheæ is immediately invested by an imperfectly preserved and undefined zone of minute cells, *b*, in which we find a number of very clearly defined leaf traces, *c*. Similar leaf traces, *c′*, are also scattered through the yet more external cortex, *m*, which obviously represents the zone that has disappeared from the sections (figs. 1, 3, 26A, 29).

The specimens just described demonstrate that, like so many of the *Lepidodendra*, the *L. Harcourtii* developed Halonial fruit-bearing tubercles at the extremities of its youngest branches, from which we may infer that its strobili must have been lateral, and more or less sessile appendages to those branches. BINNEY and HOOKER have alike described *Lepidostrobi* which they associate with *L. Harcourtii*, but I see no reason for accepting this identification.

We must next examine a most instructive specimen from Hough Hill Colliery, Stalybridge, collected by my old friend and auxiliary, Mr. GEORGE WILD, of Bardsley, near Ashton-under-Lyne, who, true to his old character, has handed over one more of his valued specimens to Mr. LOMAX and myself, allowing us to cut it in pieces in any way calculated to advance our palæobotanical researches. The specimen was one in which the large Halonial protuberances had been in two lateral series, three of these protuberances being preserved. Its leaves show that it has belonged to the Lepidophloioid group, and present every appearance of identity with the plant which is described and figured in my Memoir, Part II. ('Phil. Trans.,' 1872, pp. 209, 210, figs. 24–28), but our new specimen, being in an extremely beautiful state of preservation, teaches us much of which we were previously ignorant.

The diameter of the stem within the defined prosenchymatous zone, when uncompressed, has been about 2·5. The central xylem strand (Plate 4, fig. 30), consisting of medulla, *a*, and primary tracheal cylinder, *b*, is preserved, and corresponds in its details of structure with the ordinary Lepidodendroid forms. It gives off, from the concave crenulations of its peripheral margin, the usual leaf traces, with here and there a vascular bundle of much larger dimensions, of which the tracheæ, as seen in the transverse section, sometimes arrange themselves in an approach to a radial order (see C. N. 1952 and 1955). The inner cortex is ill preserved, but much of the middle cortex, *d*, remains, extending uninterruptedly to the prosenchymatous zone, *e*, which latter has a thickness of about ·1.† A thin external cortex, *f*, of about the same thickness as the prosenchymatous zone intervenes between it and the bases of the leaves.

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† This prosenchymatous zone evidently developed in the way illustrated in my Memoir on *Stigmaria ficoides* (Palæontographical Society's volume for 1886, Plate 8, figs. 22, 23). The meristemic zone in this *Lepidophloios* is shown in all the sections like fig. 30A, where we have the normal prosenchyma at *a*; at *c* is the outer cortex; and between the two, at *b*, the meristemic zone.

The foliage is of the true Lepidophloioid type, but the forms of the leaves vary according to the planes and directions in which sections of them are prepared. Their appearances in transverse sections of the stem are seen in figs. 30, 31, and 32, and vertical sections are shown in figs. 33 and 34. The two latter exhibit the general falcate form and arrangement which I illustrated in my Memoir II., Plate 28, fig. 27. Unfortunately, the extreme tips of the leaves now figured have been disorganized and have disappeared. Nevertheless, what remains of them is of the utmost value, illustrating, with extreme clearness, the detailed structures of this type of the Lepidodendroid foliages.

Fig. 30 illustrates the extreme differences in the forms of these leaves, as seen in transverse sections of the stem. Their almost uniform contour, as shown by sections made tangentially to the periphery of the branch is represented by Plate 3, fig. 35 (C. N. 1972–3, and 4). Turning first to fig. 35, representing one of the latter sections, we find the leaf-trace cut across at *c*, as also are the two lobes of the parichnos at *g*, *g*. The adenoid organ is cut across at *h*. In fig. 31 we have the leaf *g′* of fig. 30 enlarged seven diameters. At *c* the leaf-trace is ascending towards the apex of the leaf; on each side of its apical extremity we have, at *g*, *g*, portions of the two lobes of the parichnos; whilst at *g′* we observe the inner extremity of the leaf-trace passing through the prosenchymatous zone *e* of the cortex. (C. N. 1955.)

Fig. 32 represents a similar section (C. N. 1956) to fig. 31, but passing through a plane rather nearer the upper surface of the leaf; hence, whilst we find the upturned extremity of the leaf-trace at *c*, we have the two lobes of the parichnos at *g*, *g*, but which lobes coalesce, as they pass inward at *g′* into the prosenchymatous zone, *e*. These conditions are further illustrated by fig. 35, which represents the lower parts of these structures at the inner part of a section (C. N. 1946) like fig. 32, but further enlarged to 13 diameters. We here find the foliar bundle at *c*; the two lobes of the parichnos at *g*, *g*, but these two lobes coalesce into one at *g′*, where, as will be demonstrated shortly, these united lobes enter the prosenchymatous zone, *e*, resting upon the corresponding portion of the leaf-trace.

The two figures, 33 and 34, represent vertical sections through two of the leaves of our plant, in each of which *a* represents the injured apical extremity of the leaf, and *b* its base, broken off close to the prosenchymatous zone. These sections demonstrate that the central part of each leaf consists of a large form of parenchyma, which approaches nearer to the lower than to the upper surface of the leaf. On approaching the upper surface especially this parenchyma passes rapidly into a thick zone of small and quickly-narrowing prosenchymatous cells, forming a protective layer. In fig. 33 we find the leaf-trace at *c* curving outwards in a line closely parallel with the upper surface of the leaf, and exhibiting a small fragment of one of the lobes of the parichnos at *g*. Fig. 34 represents a similar section to 32; only, the section having passed a little on one side of the leaf-trace, it has, at *g*, cut through nearly the entire length of one of the lobes of the parichnos at *g*, which also is in close contact with the prosenchymatous upper surface of the leaf, and follows its curvatures.

The two sections, figs. 36 and 37, throw additional light upon the structures just described. Fig. 36 represents a transverse section of a leaf-trace when passing through a tangential section of the cortex, nearly in contact with the prosenchymatous zone, as in fig. 35, *g′* (C. N. 1971). The cells filling the interior of these figures of the parichnoid organs accurately represent the character of this tissue, though unfortunately they throw no light upon the functions which these organs performed when living.

Fig. 36, Plate 4, represents a section crossing the leaf-trace *c* transversely, surmounted by the corresponding section of the parichnos, *g′*, where the two pass together through the cortex immediately externally to the prosenchymatous zone, as at fig. 35, *g′* (C. N. 1971, × 50). We now find the two lobes of the parichnos united into a concavo-convex organ, in the concavity of which the leaf-trace, *c*, is in close contact with it. This is the form assumed by all these leaf-traces as they pass through the outermost cortex to enter the base of the leaf. Fig. 37 represents a section made parallel to the last, but intersecting the leaf as nearly as possible in the plane of the leaf-scar left on the leaf-cushion after the fall of the deciduous leaf (C. N. 1973, × 40). We now find the leaf-trace, *c*, and the sections of the two lobes of the parichnos, *g*, *g*, in the exact relative positions occupied by the three points mistaken by BRONGNIART for three distinct leaf-traces, and which, so far as the points *g*, *g* are concerned, have been so long without having much light thrown upon their morphology and histology. This obscurity, however, exists no longer. M. RENAULT some time ago expressed an opinion that a difference in the form of the sections of these organs constituted a generic distinction between *Sigillaria* and *Lepidodendron*. I long since rejected this conclusion, and we now have proof that the form is a variable element. The same author regarded them as gum-canals, and was of opinion that they passed through the entire cortex—an opinion which Count SOLMS is unable to accept on such evidence as M. RENAULT had then furnished ('Fossil Botany,' English translation, p. 258). My specimens, now described, certainly support the Count SOLMS' conclusions on each of these points. So far from the parichnoid organs supplying any evidence of generic, much less of class, differences between *Sigillaria* and *Lepidodendron*, the fact that the two genera alike possess these very remarkable and unique structures affords a strong additional proof of their close relationship.

In fig. 37 we find that the vertical section has passed through the curious adenoid organ at *h*. Had the section been made nearer to the base of the leaf, this would not have been the case. Both the central mass and the walls of the cavity in which that mass is lodged present the charred aspect so characteristic of this structure. We find this organ commencing near the centre of the leaf at *h* of the vertical section (fig. 33), at which point of origin its diameter is the greatest. As it proceeds outwards, in the direction of the apex of the leaf, it bends downwards towards a point near to, but somewhat below that apex.

Fig. 38 represents a portion of a vertical longitudinal section of a leaf (C. N. 1957, ×125), like fig. 33. The uppermost part of the true leaf-trace, *c*, is composed of long and generally very narrow tubular fibres, below which is a line consisting of a few elongated barred tracheæ, *c*′, which constitute the true vascular elements of the leaf-trace. I discover no distinct evidence of a phloem connected with this leaf-trace; but as it is surrounded by more or less prosenchymatous cells, *b*, *b*, a phloem may be imbedded amongst them. In this latter portion, *b*, where many of the cells, though pointed at their two extremities, become almost parenchymatous, a few of them are converted into spiral tracheæ, as at *c*″, *c*″.

There yet remain to be considered some other examples of the vascular bundles going to the Halonial and Ulodendroid fructigerous tubercles. I have already described that of *L. Harcourtii* (Plate 1, fig. 28), so far as a transverse section of it is concerned. In Plate 3, fig. 29, a longitudinal section of a corresponding bundle is seen at *b*, supplying the Halonial tubercle B.

Plate 4, fig. 29*, represents a portion of the same bundle, enlarged 40 diameters. Like the transverse section, it exhibits, at *c*, a solid strand of barred tracheæ, with no indications of intermingled cells, whilst at *c*′, *c*′ we have traces of an investing cylinder, composed of elongated cells; but I cannot positively identify these with a phloem zone, though such may be its nature.

Fig. 39 represents a tangential section through a part of the branch Plate 4, fig. 30, intersecting transversely one of the fruit-bearing tubercles in a plane near its base. We here have a very large number of tracheæ, showing a slight tendency to arrange themselves in a radial order, and with vague traces of some cellular tissue intermingled with these tracheæ (C. N. 1976, ×33). I have retained in my cabinet one of these tubercles in its integrity. At its conical apex, this tubercle exhibits exactly the same contour as those to which I have already called attention in figs. 22, 23, and 24*c*, but, in addition, the vessels constituting the large bundle corresponding to Plate 4, fig. 39, are conspicuous at its apical extremity, each trachea being filled with white earthy matter. This fact demonstrates the absolute certainty that the tubercle was once prolonged into some large deciduous appendage that has now disappeared, and which can only have been a strobilus, a large deciduous organ of any other kind being a wholly unknown thing amongst these Lepidodendroid plants.

In Plate 7, fig. 40, we have a portion of a transverse section of a tubercle belonging to a larger Ulododendroid stem than those already described. The transversely intersected divergent bundle, *l*, is again wholly tracheal, consisting of a very large number of vessels, and having a diameter of about ·07. This is immediately invested by a cortical zone of very minute cells, *k*, which, in turn, is surrounded by another zone, *m*, of similar cells of rather more variable sizes. This, again, is invested by an imperfectly completed circle of radially arranged prosenchymatous cells. Still more externally we have the ordinary cortex of the parent branch. The prosenchymatous zone encloses a circle about ·2 in diameter and is considerably external to the structures represented in the figure, which is enlarged 10 diameters. The parts contained within the prosenchymatous boundary, which latter has followed the slopes of the contracting conical tubercle, also incline inwards as they ascend towards the apex of that organ.

I must call attention to yet one more section of one of these tubercular vascular bundles (C. N. 645 B). Fig. 40A represents a longitudinal section through the bundle of another Ulodendroid tubercle, for which I am again indebted to my invaluable coadjutor, Mr. WILD. It is enlarged 18 diameters. Its tracheal bundle, *b*, consists of the ordinary type of barred vessels, but in its centre, *a*, we find three or four distinct columns of parenchymatous cells, of the same type as those common in the interior of Ferns, DE BARY's medullary cells. The periphery *d* consists of cortical cells. This development of medullary cells in the interior of a large Halonial or Ulodendroid bundle is a notable fact, which we shall shortly find to have some special significance. That the bundle is a true tubercular one is beyond question.

There still remain for consideration some additional observations respecting true Lepidodendroid strobili. BRONGNIART pointed out the necessity for the temporary retention of the name *Lepidostrobus*, only because, in his time, no clue whatever had been obtained for the identification of any one of these objects with any individual species of *Lepidodendron*, and no subsequent attempt of importance has been made to classify them. Many of the small fragments enclosed in nodules of clay ironstone, so often found at various localities, are not *Lepidostrobi*. Too frequently they are merely terminal portions of ordinary Lepidodendroid branches; besides these, true *Lepidostrobi* are not rare in such nodules, but the majority even of these are nothing more than casts, from which all structure has disappeared.

In some of my previous Memoirs I have recorded such fragmentary specimens as fell into my hands. We are now in a position to advance a little further, both in reference to their internal organization and in the identification of some of them with the parent *Lepidodendra* to which they belonged, in addition to the preceding remarks respecting the mode of their attachment to the branches of their parent trees.

In my Memoir, Part IX., and again in Part X., I figured and described a new form of fructification, remarkable alike for the structure of the strobilus and the grouping of its spores.* In Part XVI. I also described a young *Lepidodendron*, which appeared to be sufficiently distinct from all other known types to merit the provisional name of *L. Spenceri*.† Since the last of the above Memoirs was published I have obtained specimens highly suggestive of the probability that the strobilus of Memoir IX. and the twigs named *L. Spenceri* belonged to the same plant. This probability is now converted into a certainty by a specimen received from Mr. LOMAX, and now represented by fig. 41, Plate 7. It is an obliquely transverse section through a branch of *L. Spenceri* (C. N. 624*e*, × 10), but at its upper extremity, A, it bears a portion of the strobilus of Memoir IX. This part of the section is further enlarged to 17 diameters in fig. 42. *a* and *a′* are two of the characteristic sporangiophores of the strobilus, each having its small vascular bundle at the points indicated by the above letters. At *b* there is part of a sporangium, retaining some of its sporangial wall at *c*, *c*, and within it we have several very fine examples of spores, each with its peculiar investment of sterile cells described in Memoir IX. Two of these spores are represented in Plate 7, figs. 43 and 44. In 43 we have the central spherical cell of the group at *a*, containing its solitary spore, *a′*, enlarged 200 diameters. This is surrounded by a ring consisting of apparently three sterile sister-cells, *b b b*, but their exact number is not easily ascertained. These latter are distinctly hollow and inflated, but contracted to a thin margin internally where in contact with the mother-cell of the spore, and yet more so peripherally, where each one is flattened and thin.

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* Part IX., Plate 22, figs. 38 to 57; Part X., Plate 15, figs. 11 and 12.

† *Loc. cit.*, figs. 19 to 22.

In fig. 44 we have a second group like fig. 43, but here the spore is cut across, revealing at *a* an internal triangular cavity, around which is the substance of the spore, *a′*, consisting of a mass marked by a series of parallel lines. The divisions of the sterile cells, *b*, *b*, are even less distinctly defined than in fig. 43.

In Plate 8, fig. 45, we have a portion of one of these cell-clusters, enlarged 280 diameters, where *a*, *a* represents the central cell of the spore, and *b* is the zone along which one of the narrowed sister-cells was united to the central cell. These conditions are further illustrated in Plate 9. In Plate 9, fig. 46, we have one of the sister-cells detached from the central cell of the spore, but showing again, at *b*, its narrowed line of attachment to the fertile cell. At *b′ b′* is its dilated portion, and at *b″ b″* its thin outer carinal margin. Figs. 47 and 48 represent the common aspects of these spores under low powers, with the reference letters as in the other figures. Fig. 49 is a single spore, having on its surface a triangular line, which may bear some relation to the triangular centre of fig. 44.

Fig. 50 represents the most perfect vertical section through the centre of a strobilus of *L. Spenceri* that I have yet seen (C. N. 624), enlarged 9½ diameters. At *b* we have the barred vessels of the primary tracheal cylinder. At *c*, *c* are bands of the more internal cortex.* At *d*, *d* is its middle and outer cortex. The sporangiophores, *e*, are dilated at their peripheral ends, and each of the sporangia, *f*, is bounded by a wall, *f′*, consisting of a single layer of cells. It is difficult to determine with absolute certainty the point of attachment of the sporangia to the sporangiophores, but I believe that the sporangium rests upon the upper surface of its sporangiophore, and that the organic connection of the two is seen at *e′*, *e′*, at two of the upper sporangia, to the right of the figure. At both these points there is an indentation near the upper margin of the expanded sporangiophore, and opposite the same point we not unfrequently see a hook-like termination, *f″*, of the section of the sporangial wall, indicative of some interruption of its continuity, such as union to its sporangiophore would occasion. The vascular bundles supplying each of these sporangiophores pass outwards through the cortex, much in the same way as do ordinary leaf-traces; but I have not been able to detect them at the ends of these organs, where their position would demonstrate the point of union between the sporangium and its sporangiophore. I have already shown (Part XVI.) that the vegetative organs of *Lepidodendron Spenceri* present some strongly distinctive features: the present determination of its Lepidostroboid fructification brings out still more prominently the marked individuality of this rare type, and seems to justify its recognition as a distinct species.

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* See the transverse section of this strobilus in Memoir X., Plate 15, fig. 12, *d*.

In my Memoir, Part III., I described both the vegetative and reproductive organs of the plant from Burntisland to which I gave the name of *Lepidodendron brevifolium*. All subsequent experience of these beds, at Petticur, confirm my conviction that we have only found in them one species of *Lepidodendron*, and that the very youngest twigs and the matured branches, with all their specialized intermediate conditions, merely represent various stages of the growth of the same plant. If, as I believe, this is the case, we cannot hesitate to identify with it the numerous macrospores and the heterosporous *Lepidostrobi* that I found associated with the vegetative organs, and which I described in the same Memoir. In Plate 44, fig. 28, I represented four sporangia containing unmistakable macrospores, which I found at the base of a *Lepidostrobus*, the remaining sporangia of which were filled with microspores. Though so fragmentary as regards size, the specimen sufficed to establish the fact that the *Lepidodendron brevifolium* was a heterosporous form. At a later period Mr. CARRUTHERS was fortunate enough to obtain a section from the same locality, containing two superb *Lepidostrobi*: these he has kindly allowed me to figure. Each of the two figures, 51 and 52, on Plate 8 is enlarged 4⅔ diameters. It is not necessary to dwell upon the details of the structure of these *Lepidostrobi*, since they were so fully described in my Memoir, Part III. These new examples have attained to a somewhat larger size than my older ones did; but they more especially illustrate the magnitude to which the lower, or macrosporal, portion B attained, as well as the sharp boundary which, alike in 51 and 52, separates this from the upper or microsporal half A.

I have for many years endeavoured to discover some specific character by which different *Lepidostrobi* could be distinguished and identified, but thus far my efforts have been unsuccessful. At one time I thought I had obtained such specific features in the forms of the transverse sections of the sporangiophores; but I eventually found that whilst differences exist between such sections, intermediate forms occurred so frequently as to make definitions based upon them difficult, if not impossible. I have, however, figured in Plates 8 and 9 some of the more distinctive modifications that I have observed. Figs. 53 and 54 represent one of the most striking and longest known of these forms. The specimens were collected by Professor PRESTWICH, at Coalbrook

Dale, more than half a century ago, and were noticed in his classic Memoir on the geology of that Coalfield.*

Some of the principal vegetable forms collected by Mr. PRESTWICH were described and figured by the late Professor J. MORRIS, amongst which was the specimen Plate 8, fig. 54, to which he gave the name of *Lycopodites* (?) *longibracteatus.* This specimen demonstrates that the fructification was terminal at the end of a slender branch. A second of the same species, fig. 53, is a still finer one. The sporangia are conspicuous at *a*; but the most prominent feature of this type appears in the large size and leafy aspect of the terminal portions of the sporangiophores *b*. The originals of these two specimens are in the British Museum, under the care of Mr. CARRUTHERS, who kindly permitted me to figure them. They are drawn of the natural size. Fig. 55 is a vertical section of the apex of a small specimen, also in the British Museum, with leafy termination to the sporangiophores, though less conspicuously so than in figs. 53 and 54. Fig. 56 is a transverse section, enlarged six diameters, of a fine fragment of a strobilus in the same collection, but obtained from Oldham. In it we have, at *b*, well defined sections of the overlapping free ends of the sporangiophores, which have somewhat the form of similar sections of leaves of *Lepidophloios.* The sections of ROBERT BROWN's classical "Triplosporites" ('Linnean Soc. Trans.,' London, vol. 20, Part 3, T. 23, figs. B, C, D), show the radial and lateral dimensions of similar sporangiophores to be nearly equal; hence, in this example these organs were much less foliaceous than in fig. 56.

Fig. 57 is a fine longitudinal section of a *Lepidostrobus* (× 4, C. N. 1614), with radially elongated sporangia and sporangiophores. It is homosporous.

Fig. 58 is a transverse section of a fine homosporous *Lepidostrobus* from Oldham, enlarged $3\frac{1}{2}$ times (C. N. 568). In its centre we have a *facsimile* of the structures seen in the same position in the vegetative twigs of most of the young *Lepidodendra.* This portion of the section is further enlarged to 15 diameters in Plate 1, fig. 59, where we have special features of some importance. At *a* we have the space originally occupied by a medulla; at *b* is the primary tracheal cylinder, surrounded at *c* by numerous vascular bundles identical with the leaf-traces of the ordinary section of a young Lepidodendroid branch, but here destined to be distributed to the sporangiophores. One of these bundles is further enlarged in Plate 8, fig. 60. At *c*, in this figure, we have the tracheal, or xylem, elements of the bundle, and at *c′* is invariably a vacant space, which was, beyond doubt, originally occupied by the phloem portion of the bundle, which was obviously a collateral one. Where the xylem, *c*, of each bundle is still in close contact with the cylinder, *b*, as in fig. 59, this vacant space does not exist; neither are these tracheal strands as yet invested by the ring of conspicuous cells which the more external ones receive from the innermost zone of the cortex. The close resemblances of these bundles going to the sporangiophores, both in structure and origin, to the corresponding ones supplied to the leaves of ordinary Lepidodendroid branches, suggests that these sporangiophores are modified leaves. If so the term "Sporophylles" is an appropriate name to be assigned to them.

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* 'Geol. Trans.,' 2nd series, vol. 5, 1840.

Plate 6, fig. 61, represents a portion of the same *Lepidostrobus* as fig. 58, but whilst at the left-hand portion of the figure the sporangia a and the sporangiophores b are intersected tangentially, on the right hand the same organs a' and b' are cut through more radially.

Plate 6, fig. 62, represents a restoration of a radial section of this strobilus, in which we have the medulla of the central xylem strand a, at a'. At a'', a'' is the primary tracheal cylinder; b, the sporangiophores; b', expanded peltate extremity of the sporangiophore; b'', b'', the leaf-traces supplying the sporangiophores; c', the wall of the sporangium; and c, homosporous spores. In his memoir on *Lepidostrobus*,* Mr. BINNEY described and figured the above species twice over. Once (*loc. cit.*, Plate 7) from the specimen from which my sections were also derived, when he assigned to it the name of *Lepidodendron Harcourtii;* and again, in Plate 8, when he gave to it the name of *L. vasculare.* I am obliged to reject both these specific determinations. Indeed, Mr. BINNEY himself adopted the latter name, "not without doubt." As to the example figured in his Plate 57, he says that its structure "is so closely identical with that of the stem of *Lepidodendron Harcourtii* that there can be little doubt as to its having been the fructification of that plant" (*loc. cit.*, p. 48). After his death I had the opportunity of studying, very carefully, Mr. BINNEY'S entire collection of sections, and can affirm that it did not contain the smallest fragment of *L. Harcourtii.*

In his Plate 7, fig. 8, Mr. BINNEY has given a restoration of a sporangium and contiguous sporangiophore of this strobilus, but he has unfortunately suspended the former organ *under* the latter one, instead of reversing these positions.

I continue to shrink from giving specific names to examples which, in all probability, only represent types of forms reappearing in more than one species; but, as in a prevous Memoir, I still recognise the opposite inconvenience of having no concise means of referring to any object figured. With a distinct understanding as to the meaning and purpose of such names, and since the *Lepidostrobus* under consideration is rather characteristic of the Oldham deposits, I will designate the type *L. Oldhamium.*

In my Memoir, Part IX., I first called attention to the profusion of macrospores of a characteristic type, contained in the nodules obtained from the Halifax coals (*loc. cit.*, Plate 23, figs. 58–60), and in Part X. I figured and described (*loc. cit.*, Plate 15, fig. 8) a small crushed strobilus, in which these macrospores were also associated with a small fragment of a sporangium containing some microspores. This combination is better illustrated by the fragment from Halifax, represented in Plate 9, fig. 63. Here we have three distinct macrosporangia a, b, c, and three microsporangia d, e, f. In the sporangium a we have two macrospores with their characteristic fringes of hair-like appendages. In *b* there are three of these objects, and in *c* but one. The other three sporangia are crowded with microspores. I have also received from Mr. KIDSTON an abundant supply of what I have no doubt are similar macrospores, from Scotland.

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* Palæontographical Society's volume for 1870.

Knowing so little about the true form and structure of this strobilus, I do not venture to give it even a provisional name until more perfect specimens are discovered.

Plate 9, fig. 64, is an oblique vertical section through an unknown *Lepidostrobus* from Oldham, which illustrates the considerable variation observable in the sizes and forms of sections of the sporangiophores, according to their positions and the directions in which they are intersected. This seems to me to be a young fructification in which the sporangia either are not developed, or else their dimensions must have been so small, that the section has not passed through any of them.

Lepidostrobi have been found in the beds at Laggan Bay, in the Island of Arran. I have both longitudinal and transverse sections of one in the Museum of the University of Glasgow, for which I am indebted to JOHN YOUNG, Esq., the able Curator of that Museum, but they unfortunately contain no spores, and their structure is so imperfectly preserved, that no specific features can be detected in them.

Mr. BINNEY (*loc. cit.*, Plate XI.) has figured fragments of three *Lepidostrobi* from the volcanic ash of Laggan Bay, each of which is heterosporous. They are smaller than my specimen, but this may merely be a question of age, since in them the spores are preserved, whereas in mine they have all been shed. Since I have thus far obtained no evidence that we have in these volcanic deposits more than one type of *Lepidodendron* (*L. Wunschianum*), there are strong reasons for believing that it was a heterosporous form.

We have at least arrived at one result from the investigations recorded in the preceding pages; we now know that *L. Harcourtii* was not a distinct form teaching an independent and special philosophy. So far as its history is now known, it is substantially identical with that of the other known *Lepidodendra*, teaching the same truths and leading to the same inferences. We only want, in my opinion, to discover it in its arborescent condition, to place it side by side with *L. Wunschianum*, as a true typical exogenous Lycopod, and with which it has several extremely close relationships.

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* Number which the specimen figured bears in the author's cabinet.

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Plate.	Fig.		Page of the memoir where described.
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Fig 3

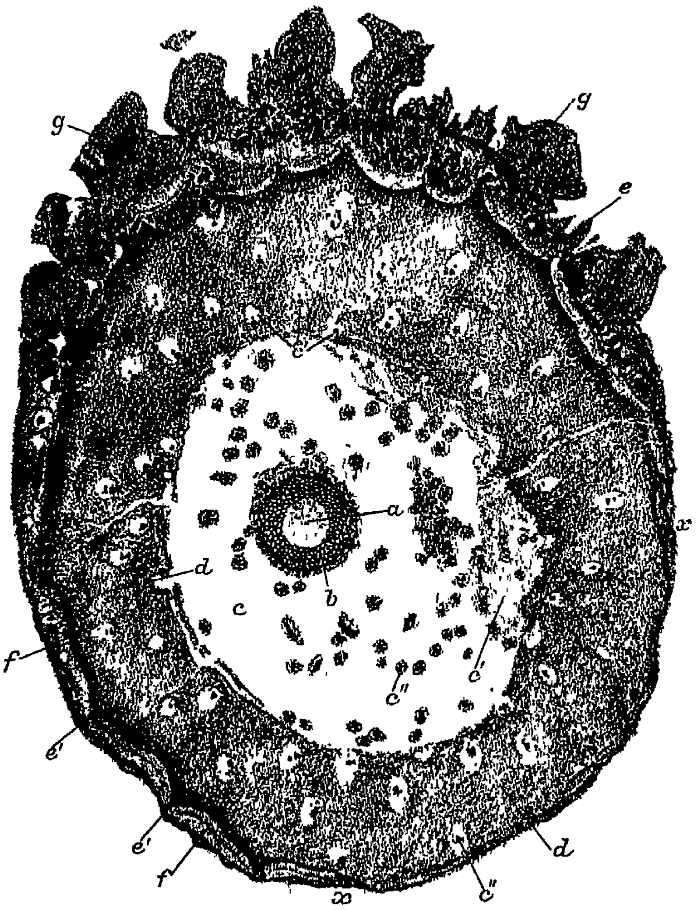


Fig 2a.

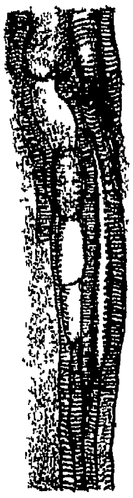


Fig. 1

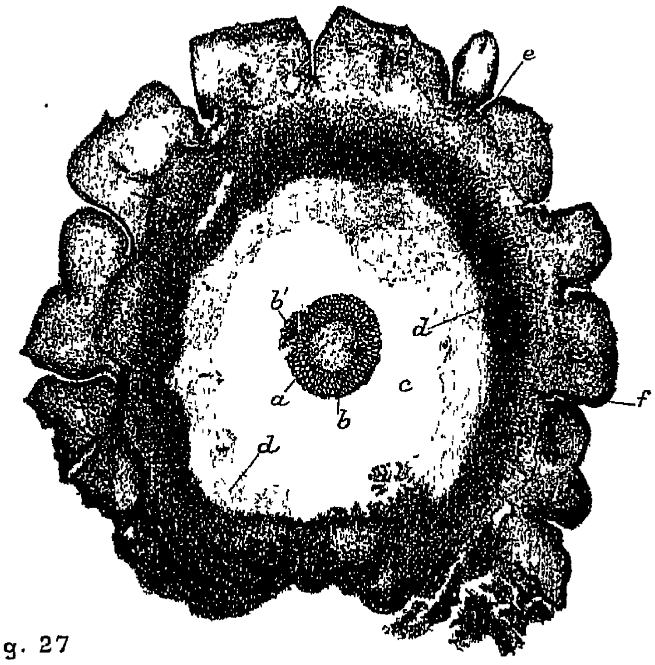


Fig. 27

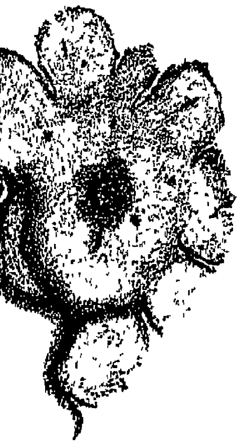


Fig. 2.

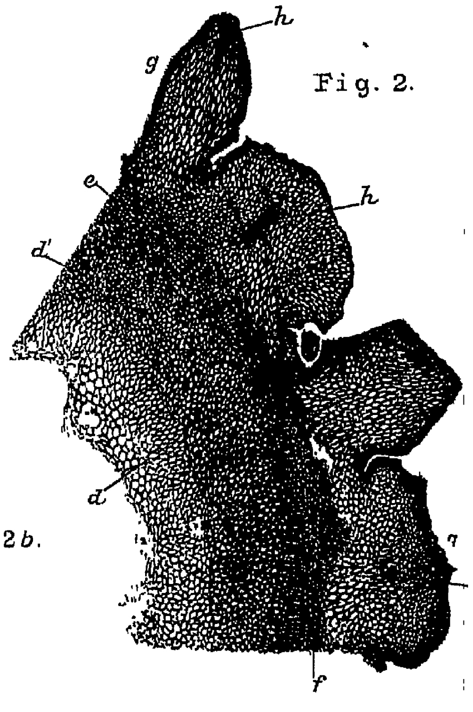


Fig. 26.

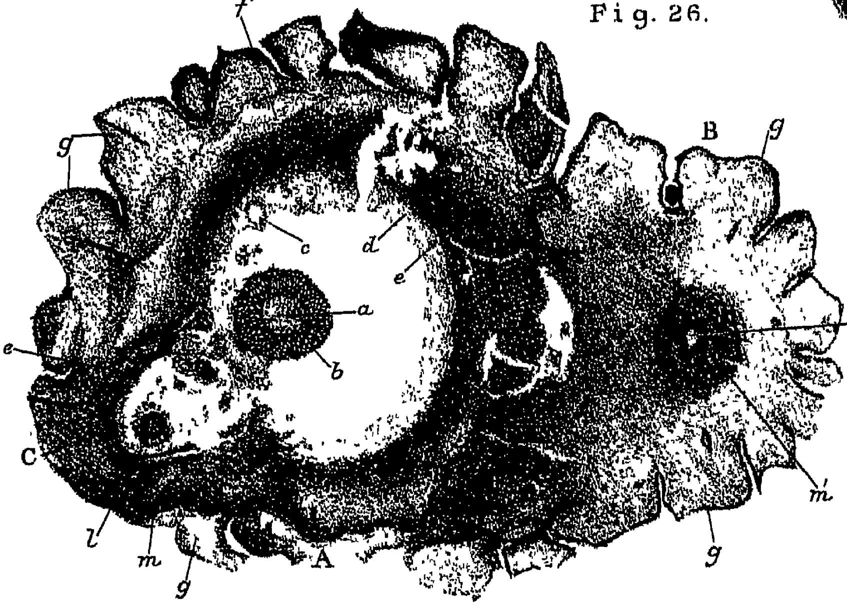


Fig. 2b.

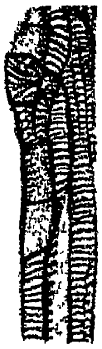


Fig 4

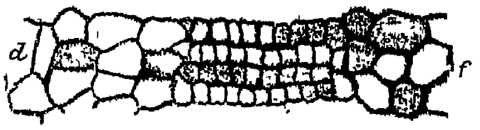


Fig. 59.

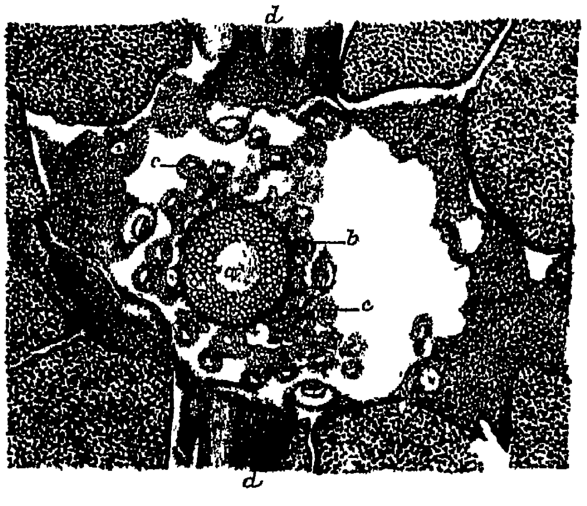


Fig. 12

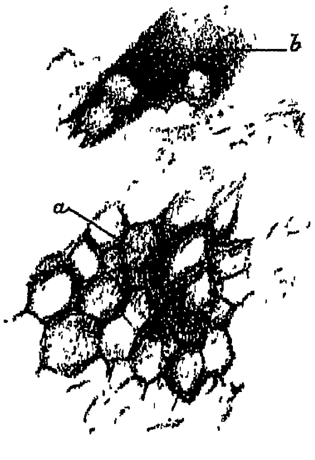
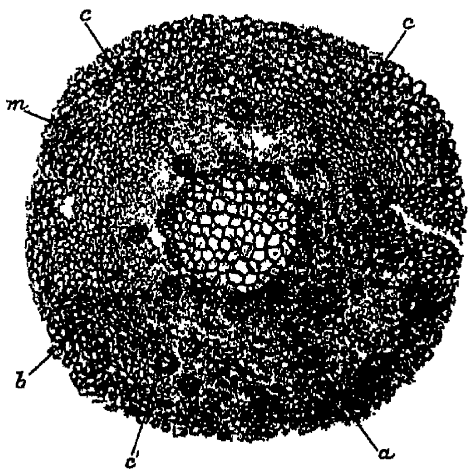


Fig. 28



W. C. Williamson, Del.

Fig 14.

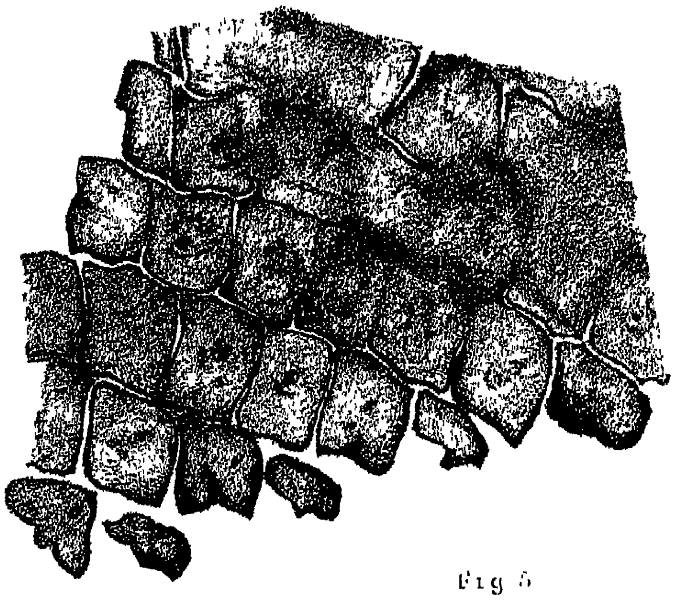


Fig. 10.

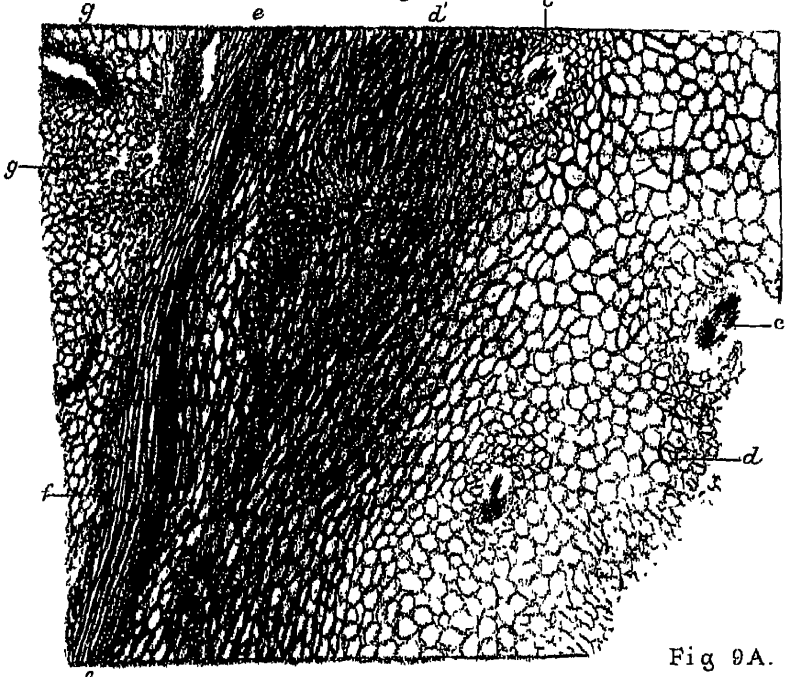


Fig 5.

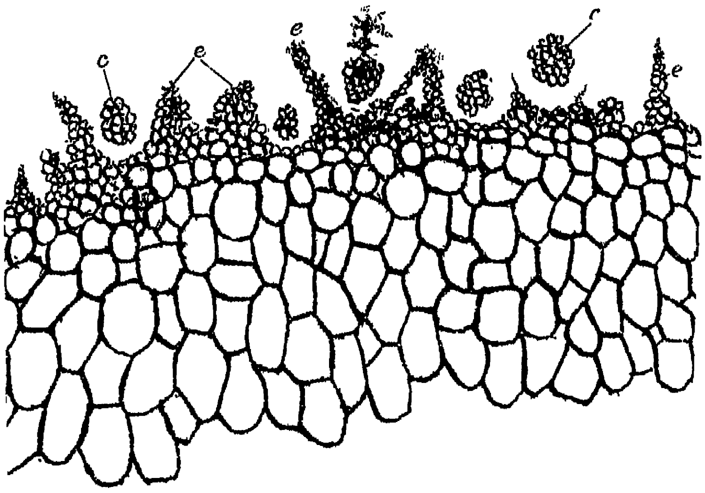


Fig 13.

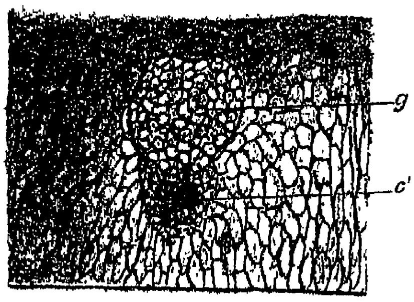


Fig 9A.

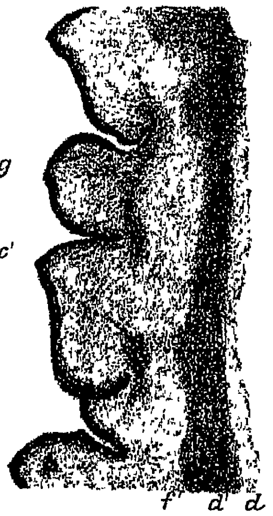
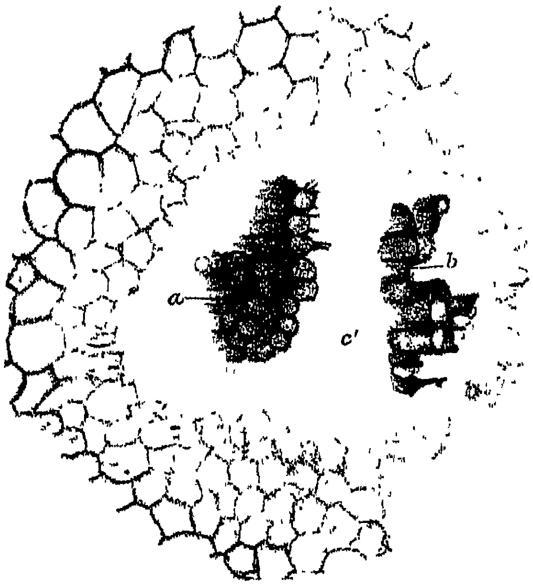
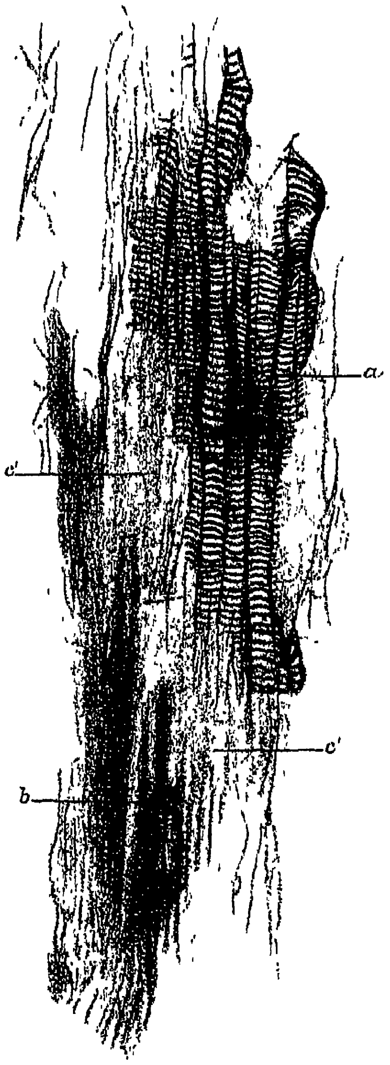


Fig 8.





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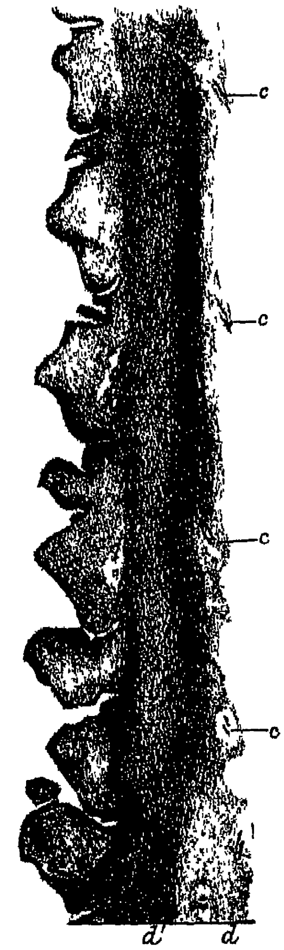

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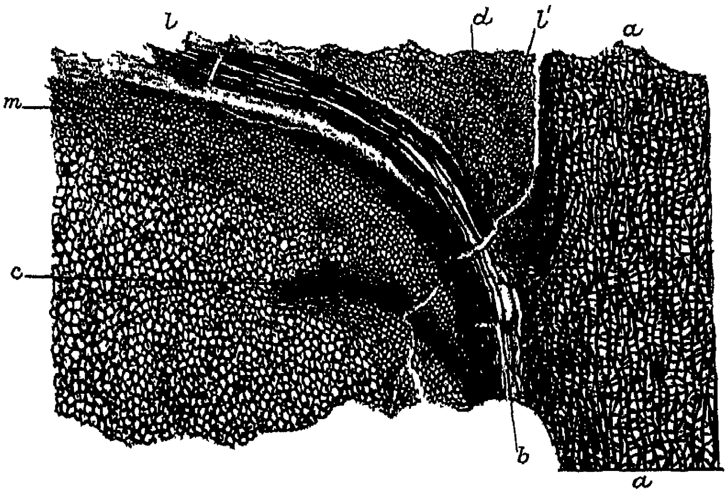

Fig. 25.

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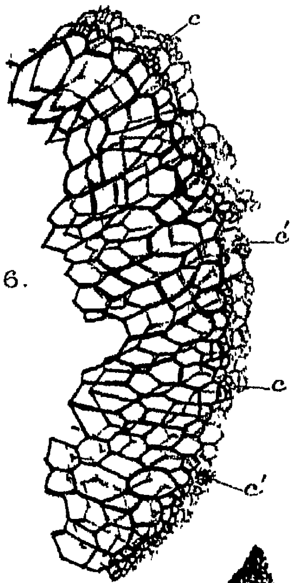

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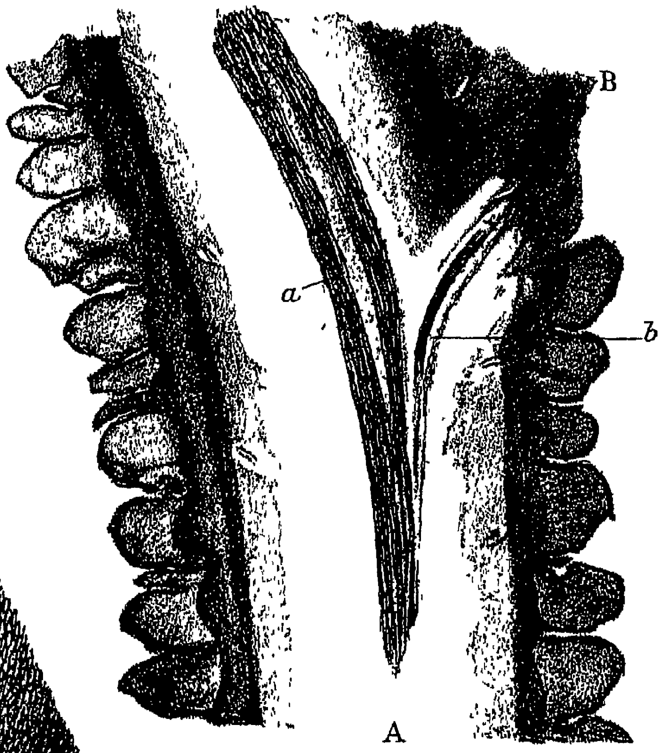

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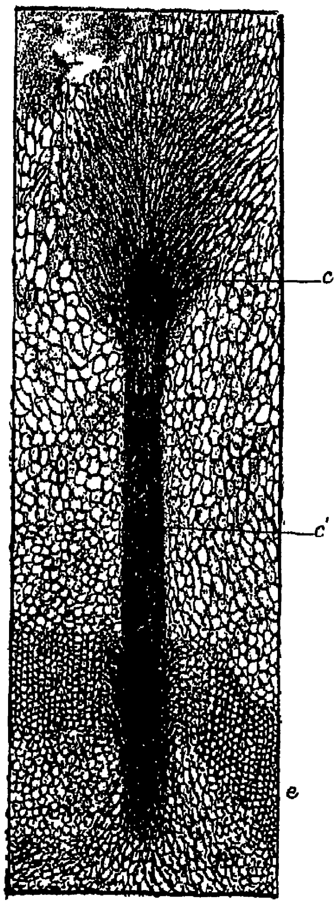

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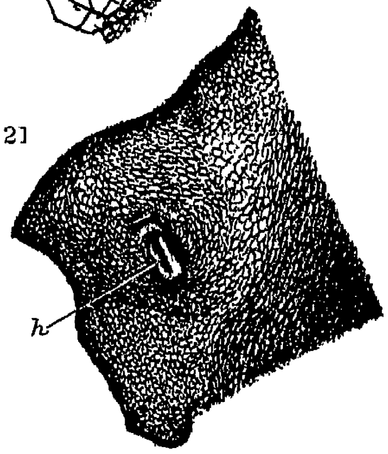

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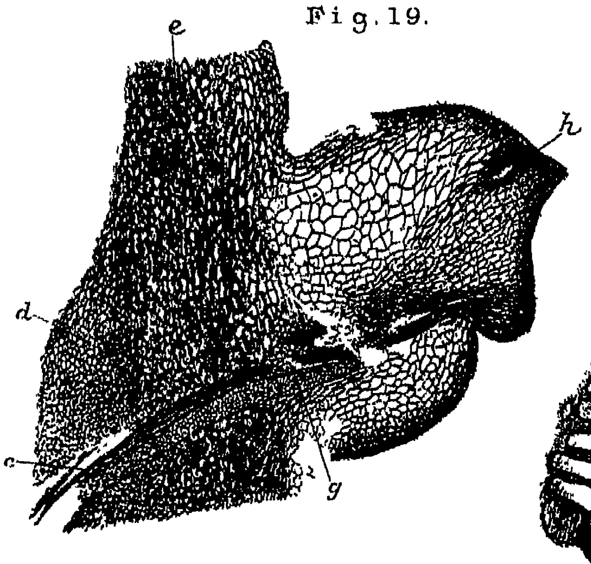

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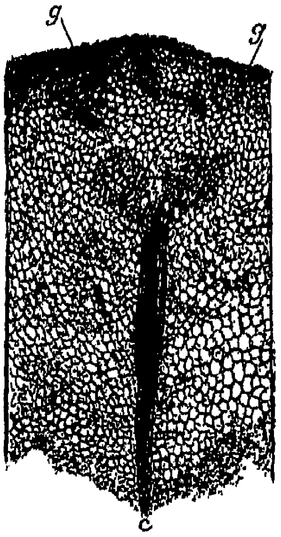

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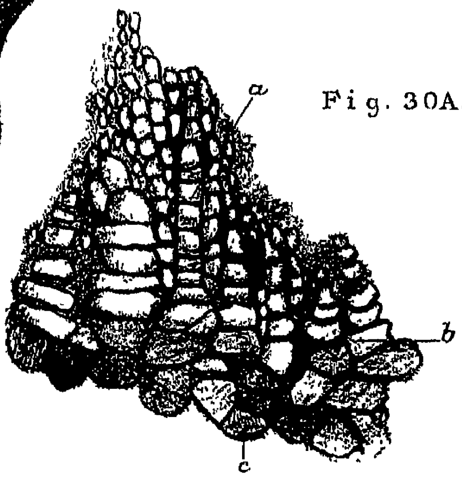

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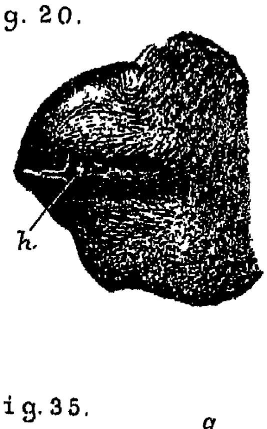

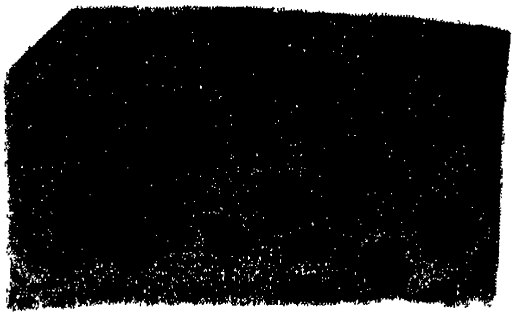

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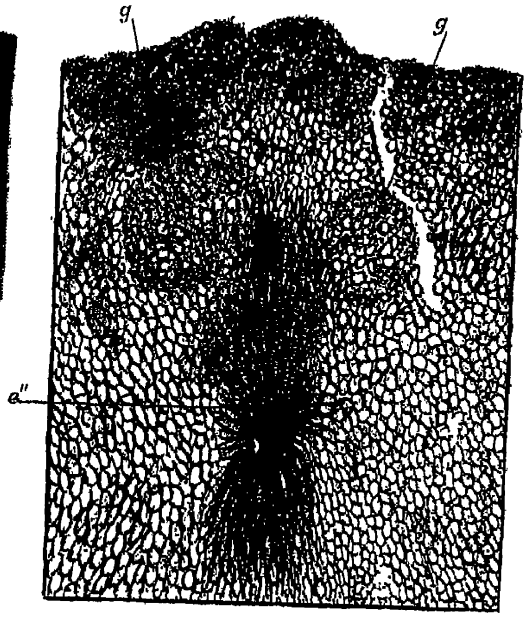

Fig. 18

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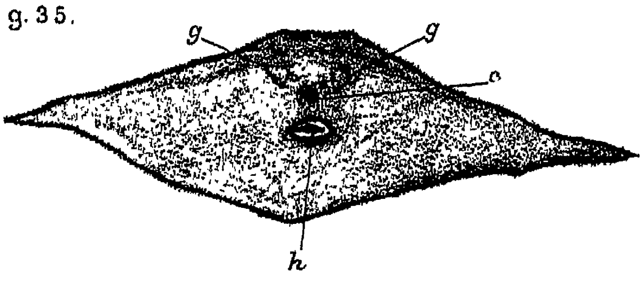

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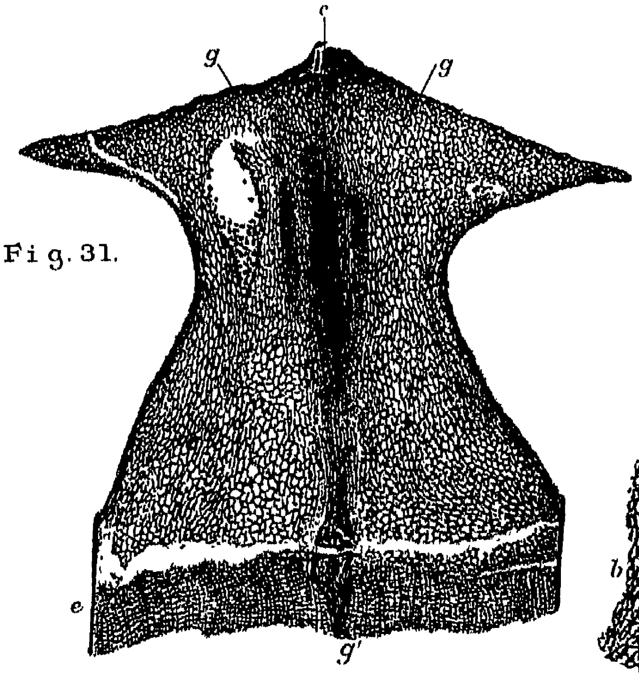

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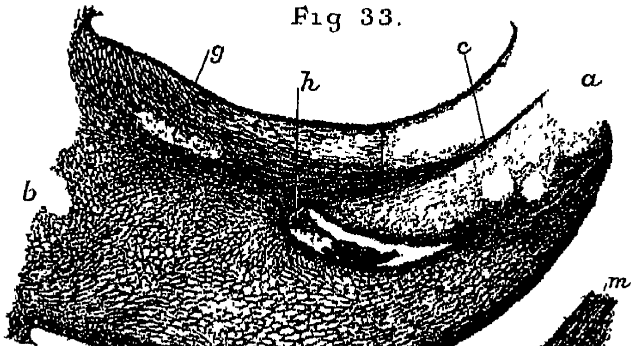

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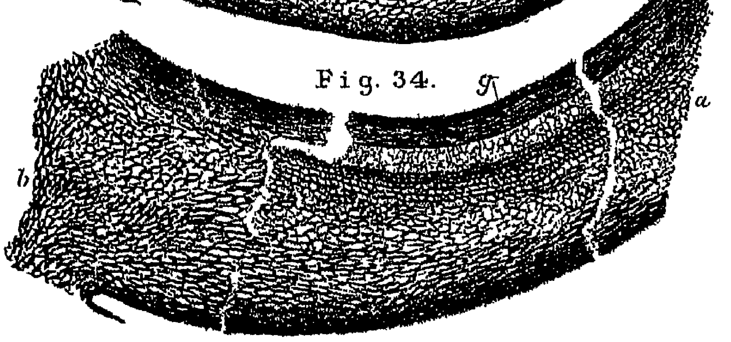

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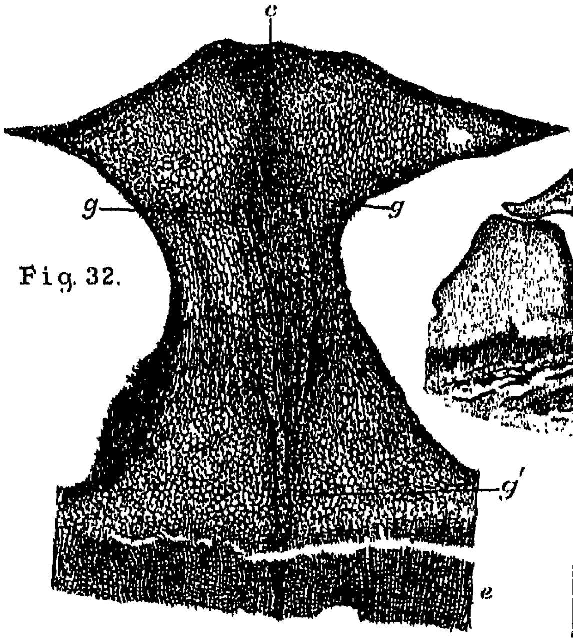

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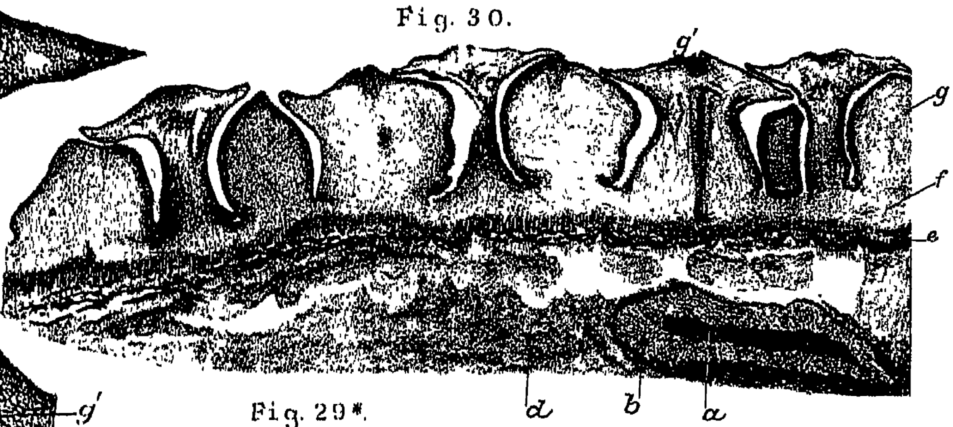

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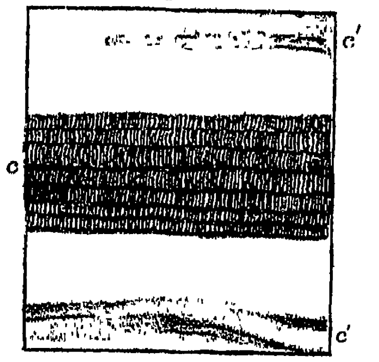

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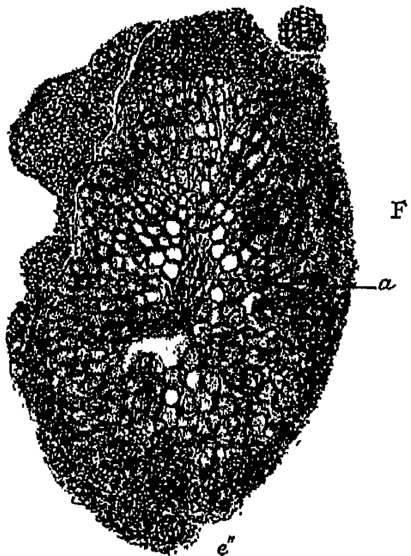

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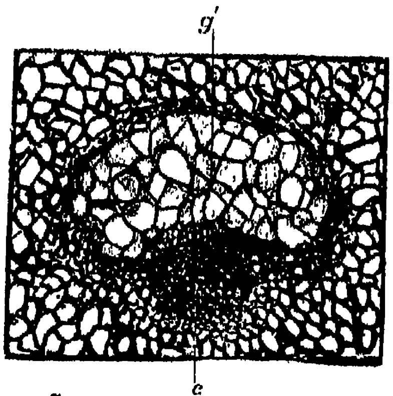

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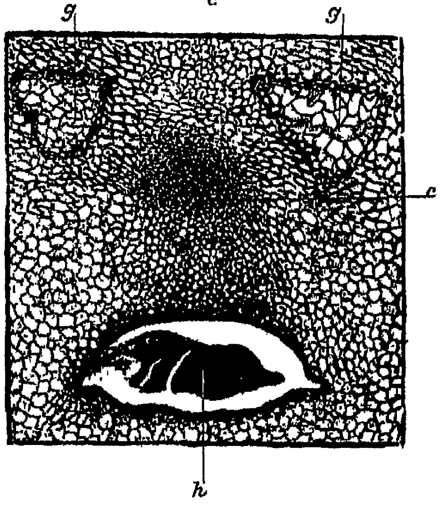

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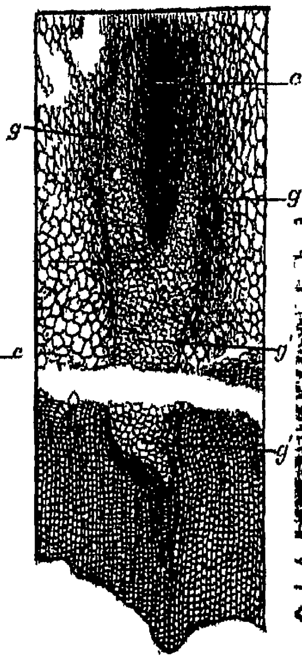

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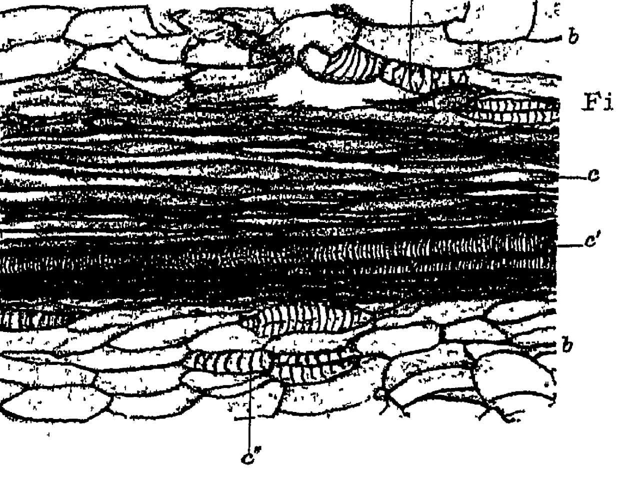

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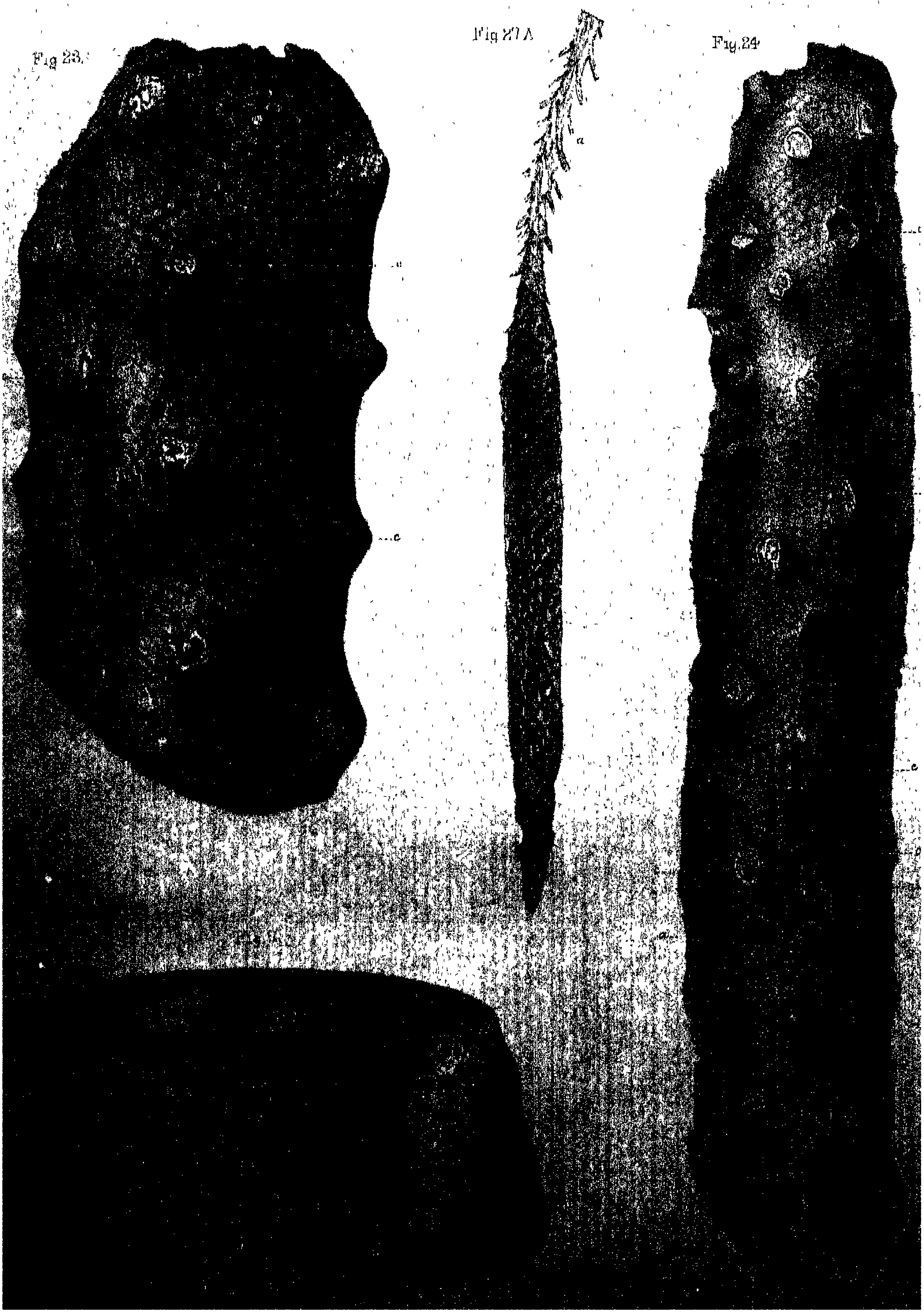
W.C. Williamson. Phil. Trans. 1893. B. Plate 5.



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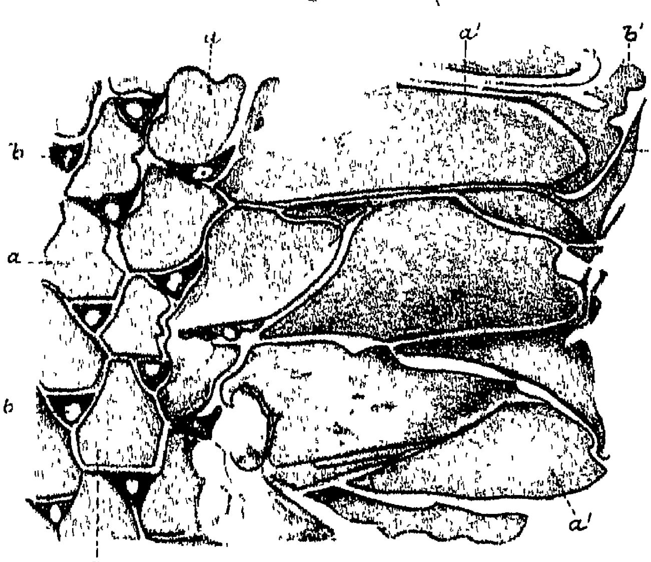

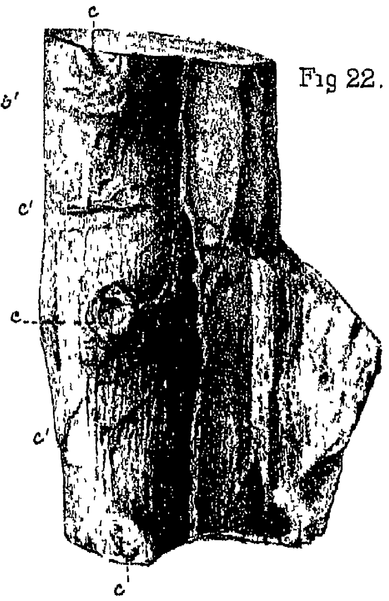

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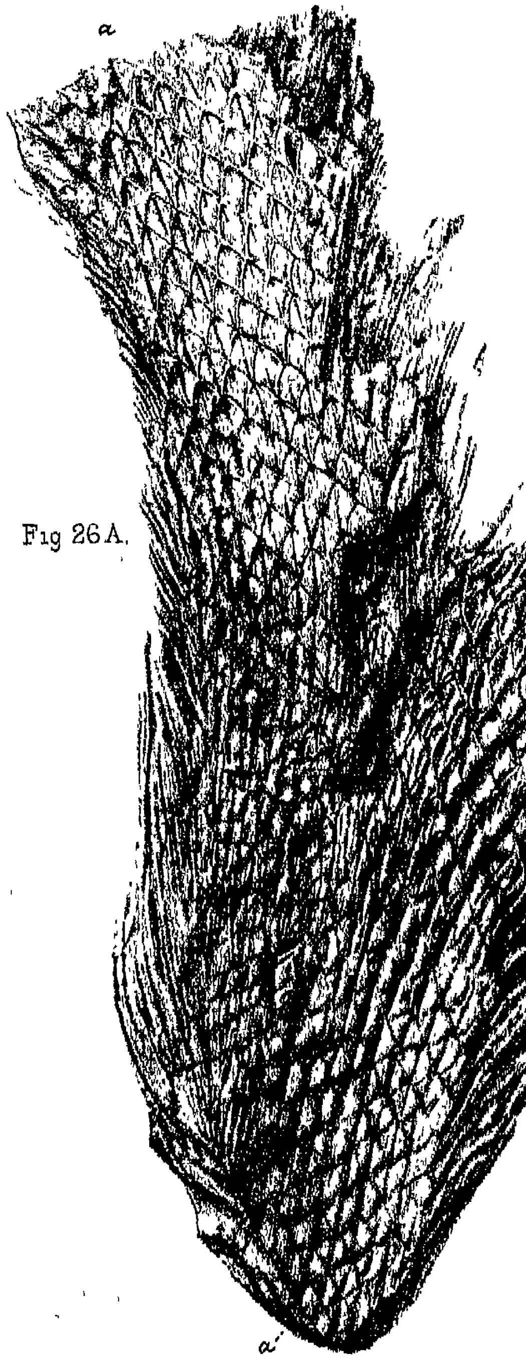

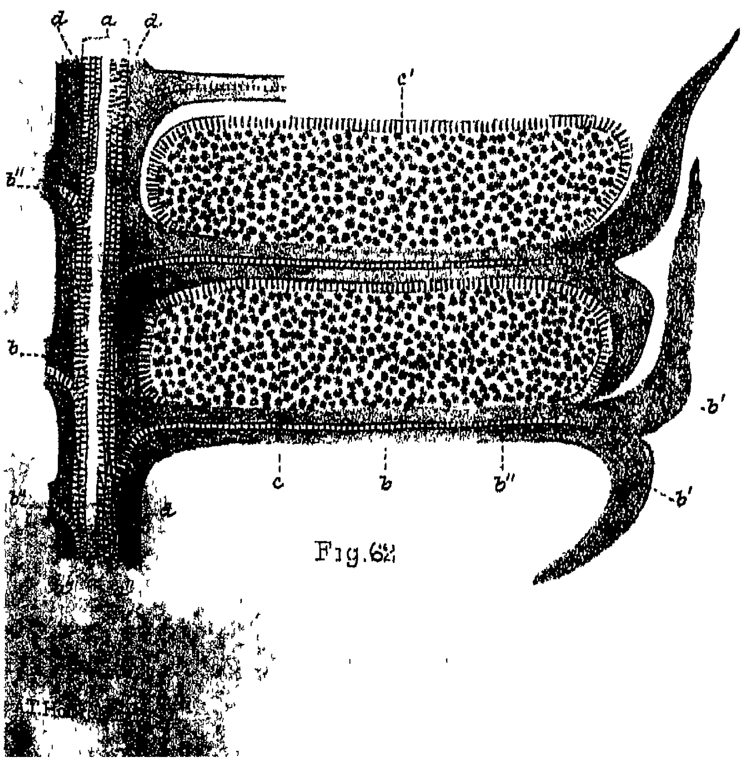

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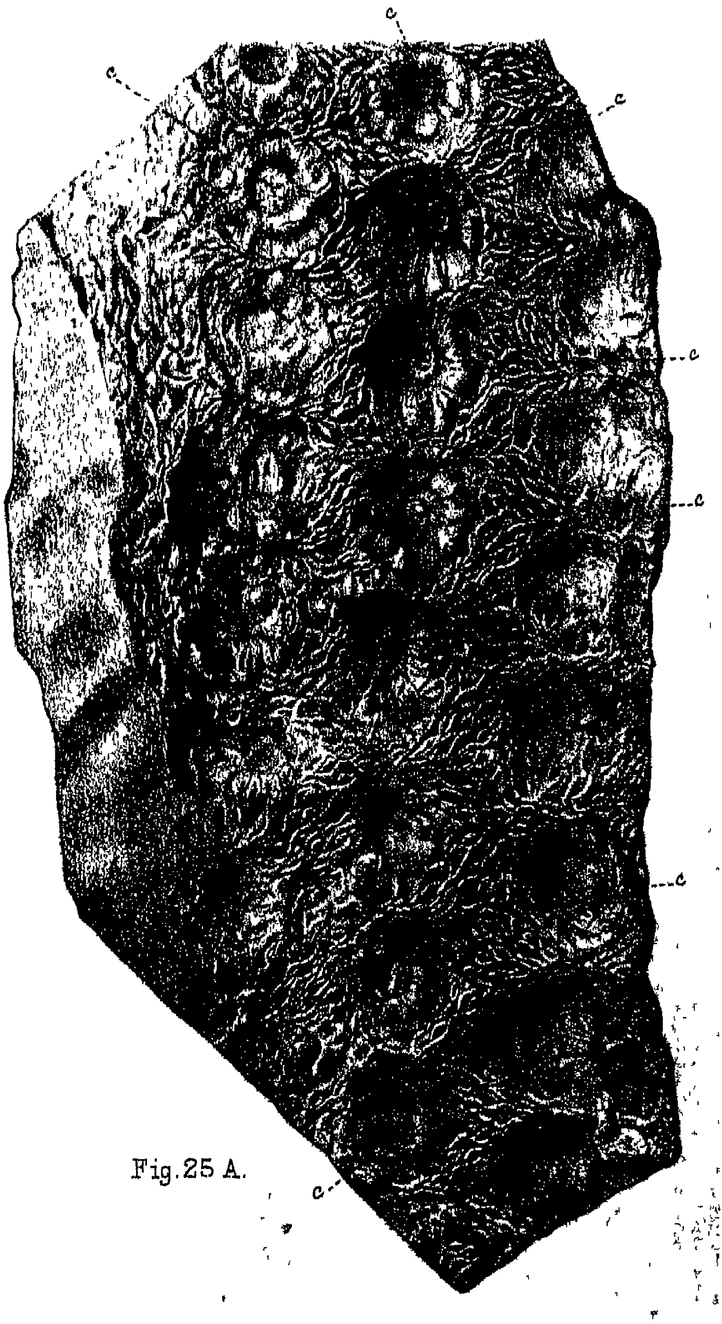

Fig.25 A.

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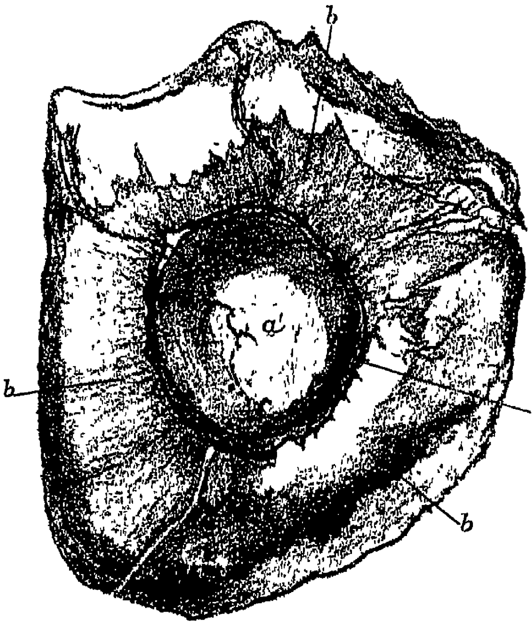
Fig. 43.



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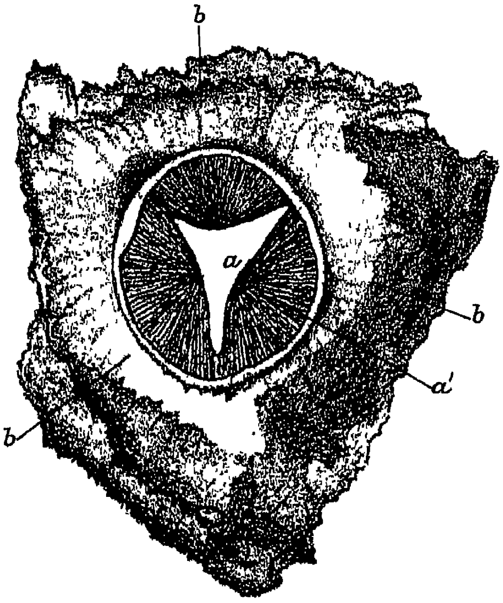

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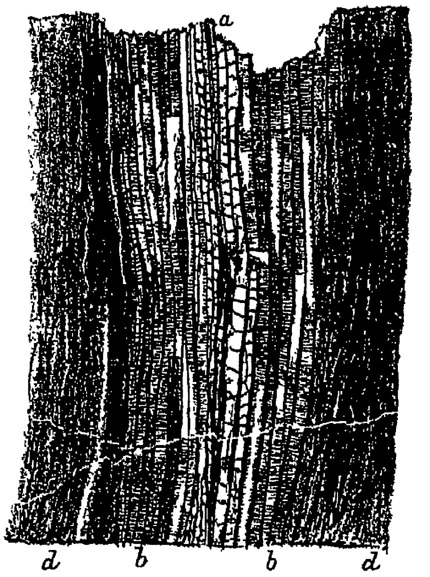

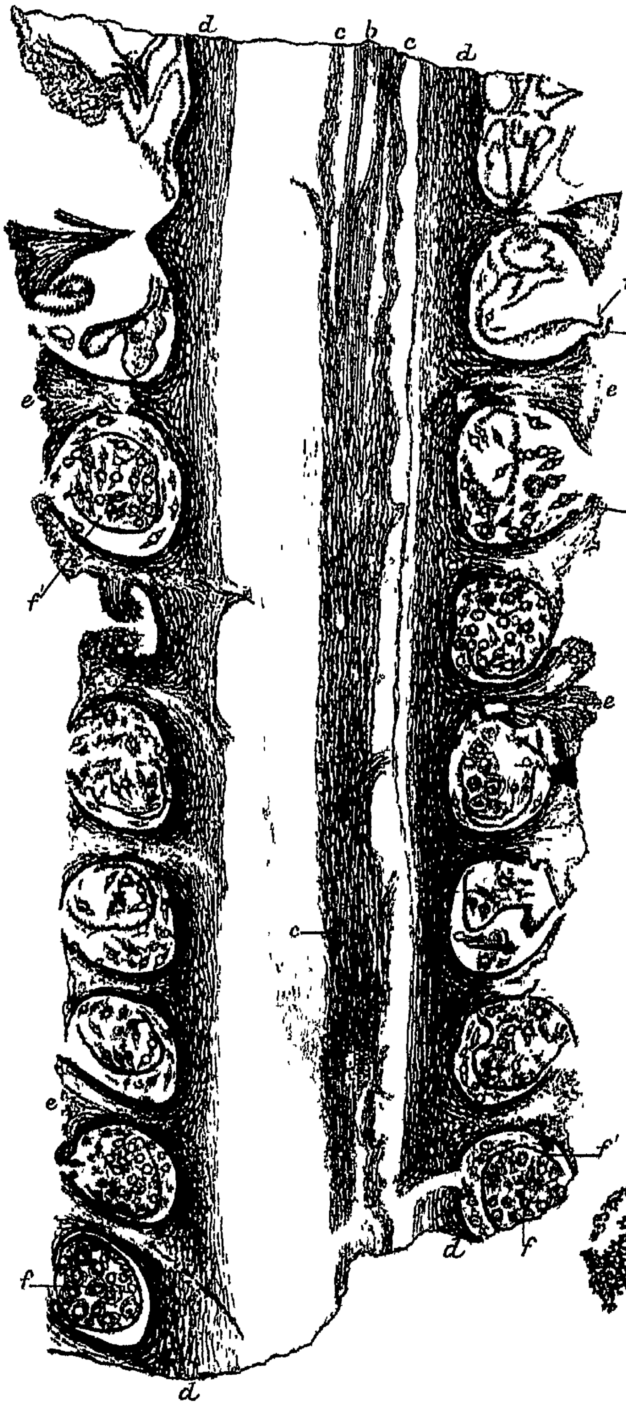

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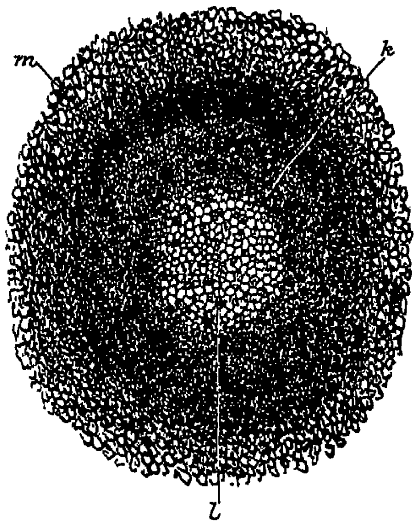
Fig. 40



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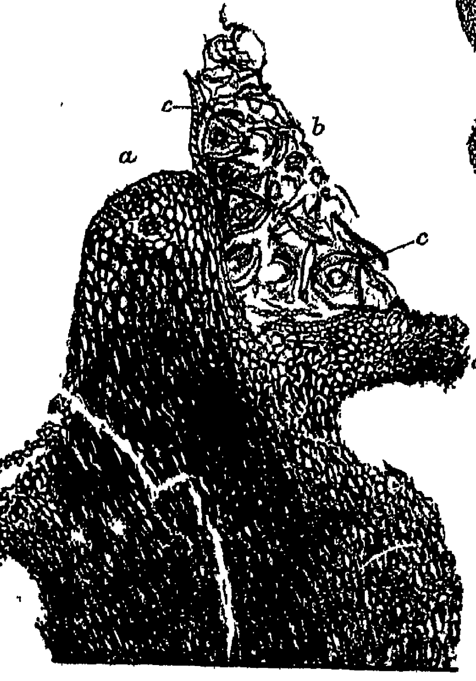

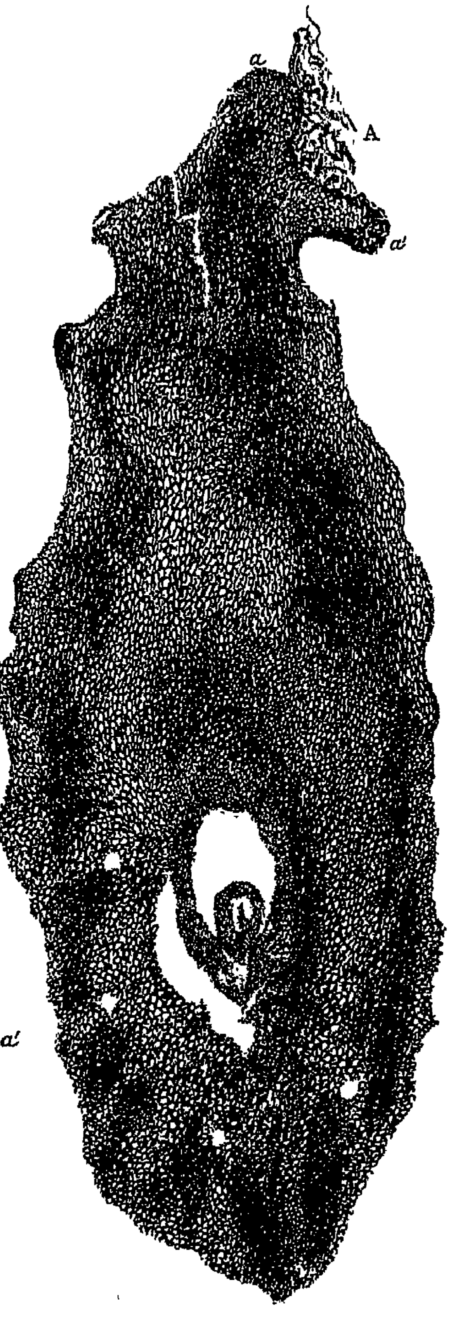

Fig. 41.

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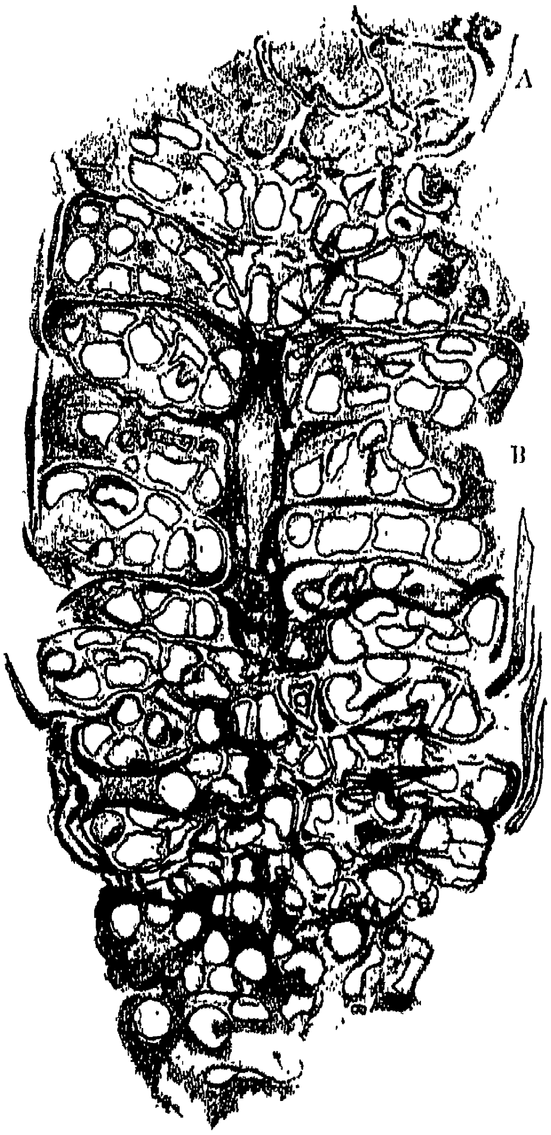
Fig. 52.



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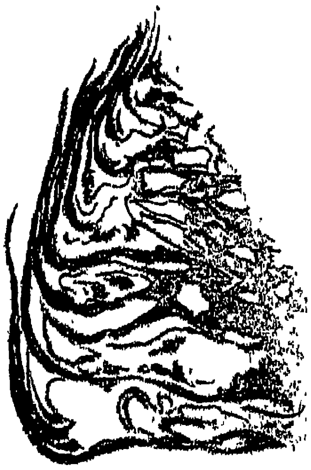

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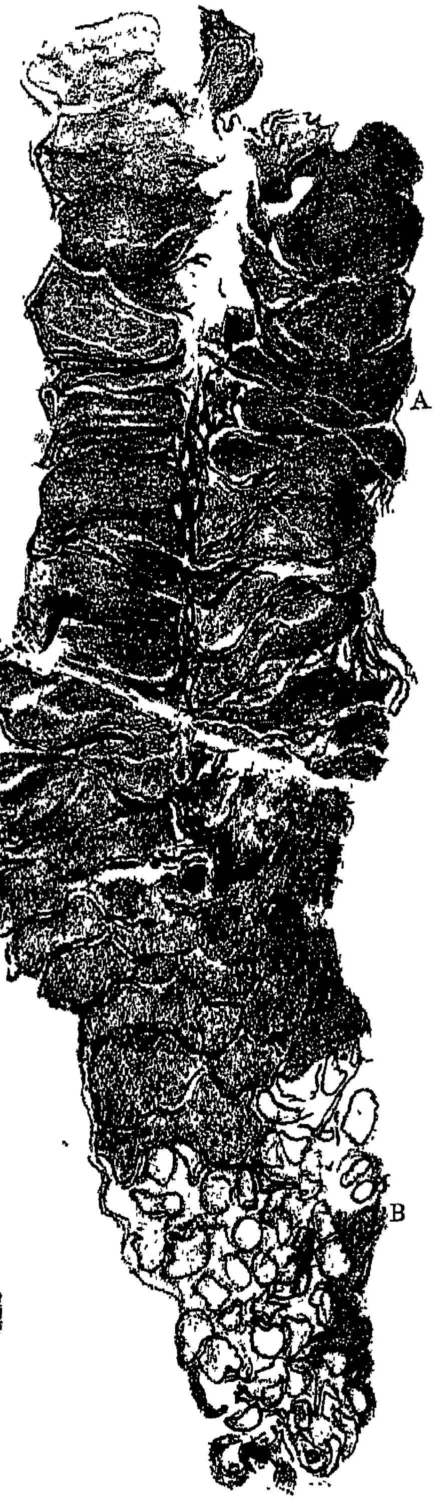

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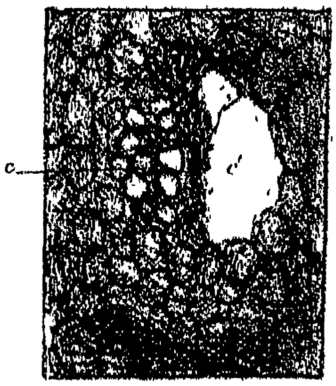

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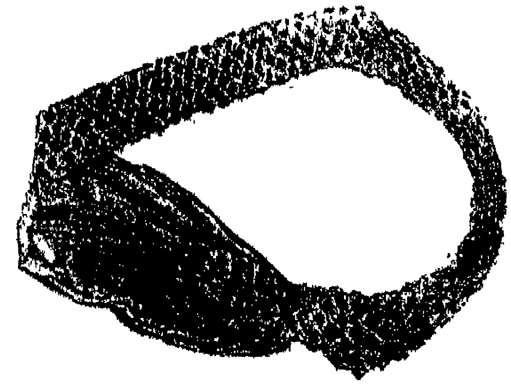

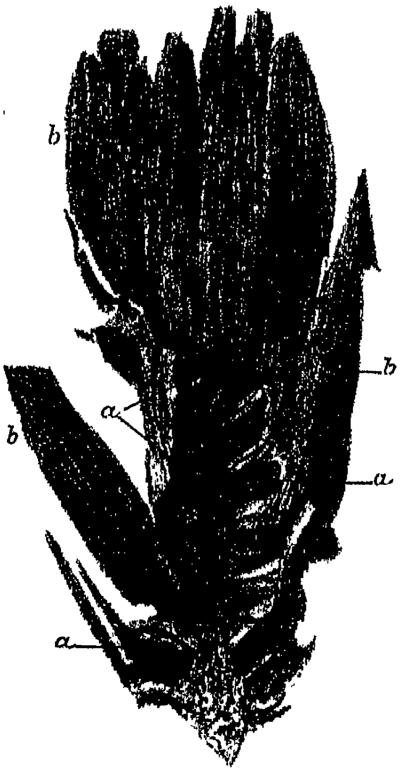

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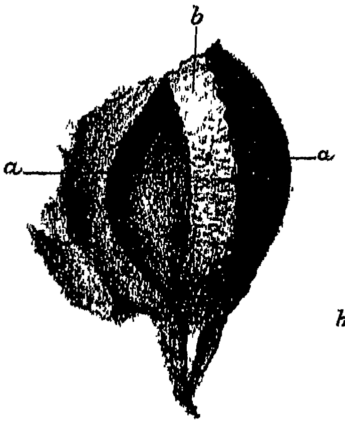

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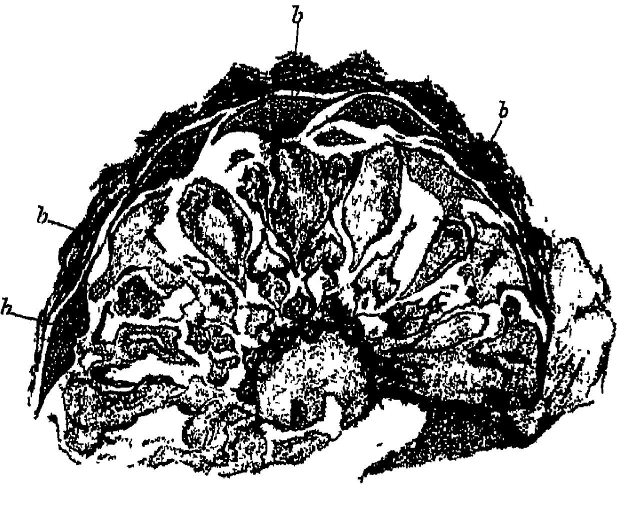

Fig. 56.

W. C Williamson, Del

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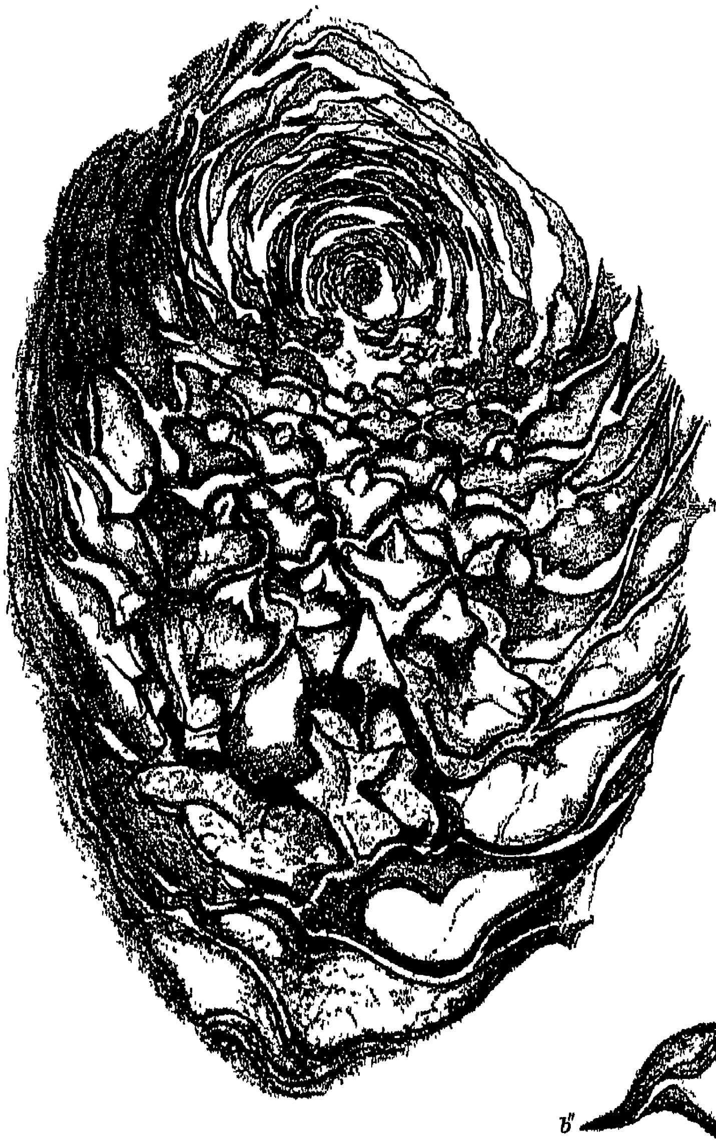
Fig. 64



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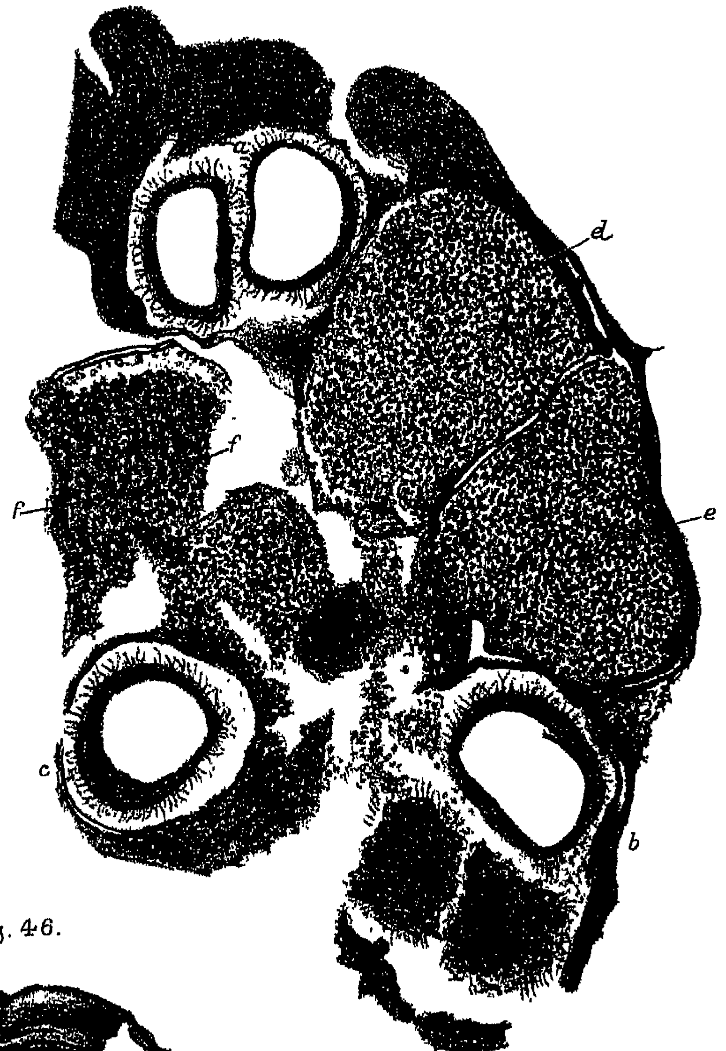

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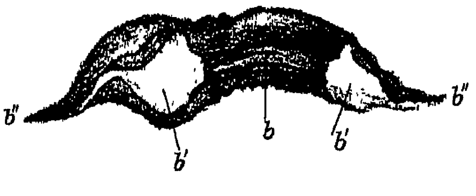

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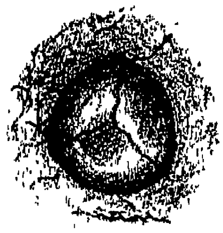

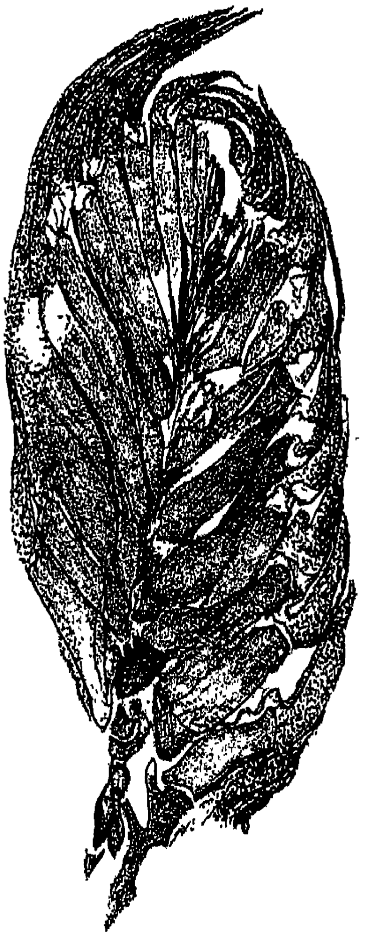

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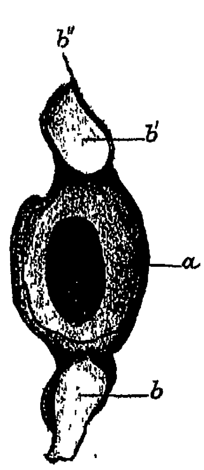

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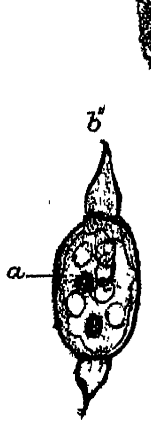

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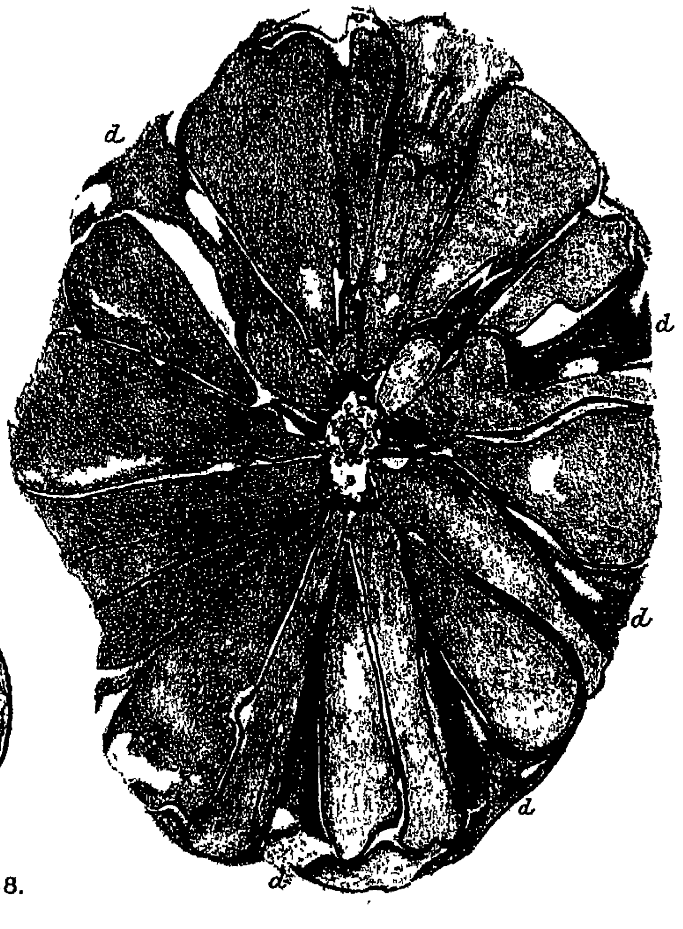

Fig. 58.

W. C. Williamson, Del.

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II. *An Experimental Investigation of the Nerve Roots which enter into the Formation of the Brachial Plexus of the Dog.*[*]

By J. S. Risien Russell, *M.B., M.R.C.P.*

Communicated by Professor V. Horsley, *F.R.S.*

Received February 18,—Read March 3, 1892.

(*From the Physiological Institute of Berlin and the Pathological Laboratory of University College, London.*)

[Plate 10.]

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I. Introduction.[†]

Numerous observers have from time to time endeavoured to determine the functional relationships between the nerve roots and the groups of muscles which they supply,

---

[*] Part of the expenses of this investigation have been defrayed by a grant from the Scientific Grants Committee of the British Medical Association.

[†] I wish to take this opportunity of expressing my most sincere thanks to Professor Gad, of Berlin, for his great kindness and courtesy in putting every facility in my way during the performance of the

11.4.93

and the subject has been approached from various standpoints. Anatomists have long endeavoured, by minute dissections, to trace the relations which exist between the nerve roots and the various nerves derived from them, together with the muscles which these nerves supply. Such a minute dissection, aided by a process of maceration in dissociating liquids, was made by W. KRAUSE* in the case of the brachial plexus. Investigations of this kind established that each nerve root sends fibres to several nerves, and that each nerve receives fibres from several nerve roots; also, that the order of derivation from above down is constant, though the exact number of roots which supply any given nerve may vary.

SCHWALBE,† in a schematic representation of the human brachial plexus, shows the inferior primary divisions of the component nerves as dividing at their origins into dorsal, or posterior, and ventral, or anterior parts, and classifies the nerves of distribution to the arm into a dorsal and ventral set, the former derived from the dorsal divisions, and supplying the extensor surface of the limb, the latter from the ventral divisions, and supplying the flexor surface.

HERRINGHAM‡ made minute dissections of the human brachial plexus in fœtuses, stillborn children, and adults, in fifty-five instances, and traced the nerve fibres from the various roots through the plexus to the nerves, and in them to their final destination. From the results which he obtained, he was able to formulate the following laws:—

> "Law I.—Any given fibre may alter its position relative to the vertebral column, but will maintain its position relative to other fibres."
>
> "Law II.—A. Of two muscles, or of two parts of a muscle, that which is nearer the head-end of the body tends to be supplied by the higher, that which is nearer the tail-end by the lower nerve."
>
> "B. Of two muscles, that which is nearer the long axis of the body tends to be supplied by the higher, that which is nearer the periphery by the lower nerve."
>
> "C. Of two muscles, that which is nearer the surface tends to be supplied by the higher, that which is further from it by the lower nerve."

---

earlier of these experiments, for the kind interest which he took in my work, and for his great willingness always to verify the results which I obtained from time to time. The original instrument devised to control certain movements of the limb while others were left free to take place, was made under his supervision, and almost entirely on the plan which he very kindly suggested. It is impossible for me to thank him warmly enough for the amount of trouble and personal inconvenience to which he put himself on my behalf.

To Professor VICTOR HORSLEY I owe a similar debt of gratitude, for allowing me to complete these investigations in the Pathological Laboratory of University College, and for his exceedingly kind and invaluable suggestions as to the general plan on which this paper should be arranged.

* KRAUSE, "Beiträge zur Neurologie der Oberen Extremität," 1865.

† SCHWALBE, "Lehrbuch der Neurologie," Erlangen, 1881, p. 914.

‡ HERRINGHAM, "Proceedings of the Royal Society," 1886, vol. 41, p. 423.

He also found that the sensory nerves obeyed the following rules :—

"A. Of two spots on the skin, that which is nearer the pre-axial border tends to be supplied by the higher nerve."

"B. Of two spots in the pre-axial area the lower tends to be supplied by the lower nerve, and of two spots in the post-axial area the lower tends to be supplied by the higher nerve."

PATERSON,[*] from dissections of the brachial plexus in the Porcupine, Koala, Rat, Rabbit, Guinea-pig, Cat, Camel, Brindled Gnu, Capucinus and Entellus Monkey, found that in five of these animals five nerves entered into the formation of the plexus; in four, four nerves gave rise to it; and in one (Entellus Monkey) six nerves were concerned in its formation. The nerves constantly present were the sixth, seventh, and eighth cervical, and the first dorsal; those not constant being the fourth, present in the Entellus Monkey, and the fifth, present in five cases. He was able to deduce the following conclusions from a comparison of the results by his dissections :—

1. The inferior primary divisions of the nerves entering the plexuses divide into dorsal and ventral trunks.

2. The dorsal divisions of the nerves always combine with dorsal divisions, the ventral divisions with ventral divisions to form the nerve of distribution.

3. The essential constitution of a nerve of distribution consequently never varies. A nerve arising from a combination of the dorsal divisions of certain nerves in one animal is never found in another animal to spring from the ventral divisions of these or any other nerves. The same rule applies to nerves derived from ventral divisions.

He further goes on to show that those parts of the limb derived from the dorsal surface of the embryonic limb, are supplied by nerves from the dorsal divisions, while those parts of the limb derived from the primitive ventral surfaces are supplied by nerves derived from the ventral divisions.

He suggests that in an early period of development the arrangement of the nerves is simple, supplying the bud representing the limb. The more pre-axial nerves are said to supply the pre-axial portion of the limb, the more post-axial the post-axial portion of the limb, while the inferior primary division of each nerve divides into a dorsal and ventral branch, to supply the dorsal and ventral surfaces of the embryonic limb. As the muscular system becomes developed and the changes take place in connection with the production of the adult condition, so the embryonic nerves are supposed to become more differentiated and complicated in their arrangement.

To ERB[†] is due the credit of having first recognised and drawn attention to the paralysis of a certain group of muscles depending on an affection of certain nerve roots. In all ERB's cases the deltoid, biceps, and brachialis anticus were affected; in two in which it was examined, the supinator longus was also found affected, as was also the supinator brevis. He ascribed the condition to an affection of the fifth and sixth cervical nerve roots; a conclusion which he afterwards verified by finding a motor point in the neck, stimulation of which produced contraction of the group of muscles he had formerly found paralyzed in combination.

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[*] PATERSON, 'Studies in Anatomy,' Owens College, 1891, vol. 1, p. 135.

[†] ERB, "Ueber eine eigenthümliche Localisation von Lähmungen im Plexus brachialis." ('Verhandl. des Heidelb. naturhist.-med. Vereins,' N.S., 1, 2, 1874.)

Since ERB's publication, numerous similar instances have been recorded. A. KNIE[*] published a case in which the motor portion of the fifth cervical nerve root was divided during an operation. Immediately after the operation, the movements at the shoulder were unaffected, there was paralysis of the movements at the elbow joint, while those below the elbow remained normal. Exact differentiation of the muscles involved, however, was impossible, on account, apparently of diffuse changes.

A valuable series of cases of injury to the cervical region of the cord in Man at different levels, has been published by THORBURN,[†] which go to prove the relationship between the grouping of fibres in the nerve root and the respective levels of the spinal cord from which they are derived.[‡]

II. HISTORICAL ACCOUNTS OF PREVIOUS EXPERIMENTAL RESEARCHES.

Experimental investigation in the lower animals is not only the most rapid, but also the most precise means at our disposal of ascertaining the functional motor relations of the nerve-roots. By this means our knowledge has been greatly increased, notably by the work of FERRIER and YEO in this country, and that of FORGUE in France.

MÜLLER[§] and VAN DEEN,[‖] from experiments on the crural plexus of the Frog, together with a consideration of KRONENBERG's experiments, to be afterwards referred to, came to the conclusion that, as far as the motor parts of the roots of the plexuses are concerned, the plexuses were arrangements for conveying fibres to each muscle from different parts of the brain and spinal cord, and that in them the sensory and motor fibres were possibly mixed to suit the wants of the areas which the nerves supply.

KRONENBERG[¶] found that mechanical or electrical stimulation of each of the cervical roots which innervate the fore extremity of the Rabbit, resulted in nearly every muscle of the limb being thrown into contraction. His views as to the function of a plexus were identical with those of MÜLLER.

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[*] KNIE, 'St. Petersburg Med. Woch.,' 1889, Nr. 24, p. 215.

[†] THORBURN, 'Brain,' January 1887 and October 1888.

[‡] DUCHENNE had previously recognised a form of "obstetrical" paralysis in which the deltoid, infraspinatus, biceps, and brachialis anticus were involved; and in addition several other cases of localized paralysis were recorded by him, but without any attempt to interpret any of them by the light of anatomical facts.

[§] MÜLLER, 'Handbuch der Physiologie des Menschen,' vol. 2, 1834, p. 685.

[‖] VAN DEEN, 'De differentia et nexu inter nervos vitæ animalis et organismi,' Leyden, 1835.

[¶] KRONENBERG, 'Plexuum Nerv. Struct. et Virt.,' Berol., 1836.

Panizza,* by section experiments on the crural plexus of Frogs and Goats, was led to the same conclusion. He found that the amount of weakness produced in an extremity depended on the number of roots divided, and that, in order to obtain complete paralysis, all the roots must be divided. He therefore concluded that each root was capable of keeping all the movements intact, and that the difference between the action of one and all the roots supplying an extremity was merely one of degree.

Peyer† exposed the muscles by dissection, and noted which contracted on stimulation of each cervical root in the Rabbit. The sensory distribution he ascertained by dividing all the roots with the exception of one, and then finding in which area cutaneous stimulation resulted in reflex movements. He found that the group of muscles supplied by each root was a complex one, and not a simple one such as that of flexors or extensors; further, that each muscle was supplied by more than one root as a rule. He also came to the conclusion that the sensory roots were distributed to the cutaneous surfaces overlying the muscles supplied by the corresponding motor root.

Krause,‡ by his researches, confirmed more or less those of the last observer. His method of procedure was that of tracing degenerations consequent on division of a given root in the Rabbit, along the motor and sensory fibres. He once divided the sixth and seventh cervical roots in the Monkey, and found that no degeneration followed in the ulnar and median "sensory nerves" of the hand, and concluded, therefore, that they derived their supply from the eighth cervical and first dorsal.

Ferrier and **Yeo**§ found that in the Monkey stimulation of the individual roots determined not only contraction of various muscles, but a group of muscles in synergic combination, the effect of which was to produce a highly co-ordinated movement, as **Remak** had supposed must be the case in Man. From this they concluded that section of each motor root would determine paralysis of the corresponding combined movement, but not necessarily the individual muscles involved, for, as many of the muscles are innervated by more than one root, the amount of paralysis of any given muscle would depend on the degree of motor innervation by the root divided, and that, therefore, though weakened, they would be still capable of entering into other combinations.||

Bert and **Marcacci**¶ obtained results in Dogs and Cats which essentially agree with the observations of the last-named experimenters. But, inasmuch as these

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* **Panizza**, 'Annali Universali di Medicina,' 1834.

† **Peyer**, 'Zeitschrift für Rationelle Med.,' N.F., vol. 4, 1854.

‡ **Krause**, *loc. cit.*, and 'Anatomie des Kaninchens,' 1868, p. 247.

§ **Ferrier** and **Yeo**, 'Proceedings of the Royal Society,' 1881, vol. 32, p. 12.

|| I do not add the details of the muscles supplied by each root, as observed by **Ferrier** and **Yeo**, inasmuch as their observations relate to the Monkey and not to the Dog.

¶ P. **Bert** and **Marcacci**, 'Gazette Med. de Paris,' 1881, p. 512.

observations were made with regard to the lumbo-sacral plexus of these animals, a detailed account of the experiments is not called for here.

FORGUE,* from the results of his investigations in the Frog, Dog, and Monkey, formulated the following three laws:—

1. Each root supplies the two opposite surfaces of the limb, the anterior and the posterior.

2. As one approaches the dorsal roots, the muscular contractions evoked involve the inferior segments of the limb.

3. At the same time, the contractions progressively involve the muscular masses proceeding from the radial to the ulnar side of the limb. He also adds: "It is a secondary law that the superficial layers are supplied before the deep."

This observer stimulated the respective nerve roots, after exposing and dividing them in the neural canal, in order to obtain the combined effect produced by stimulation of the whole root, but for the exact observation of the individual muscles related to each root, he resorted to stimulation of the branches arising from the different nerve-roots. All the roots supplying the plexus were divided before any of them were stimulated, and every other care was taken to preclude the possibility of error from diffusion of the electric current by which the roots were stimulated. The muscles were exposed by dissection in order to allow of direct observations of them during their action. In this way he determined the following arrangement of muscles in connection with the various nerve-roots of the brachial plexus in the Dog.

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* FORGUE, 'Distribution des Racines Motrices dans les Muscles des Membres,' Montpellier, 1883.

Anterior surface of limb.	Posterior surface of limb.
VI. Cervical nerve root Humero-mastoid Subscapularis Biceps Coraco-brachialis Brachialis anticus	Supraspinatus Infraspinatus
VII. Cervical nerve root Subscapularis Biceps Coraco-brachialis Brachialis anticus Pronator teres Palmaris longus	Supraspinatus Infraspinatus Deltoid (scapulo-acromial) Teres major Latissimus dorsi Serratus magnus Outer and inner heads of triceps Extensor carpi radialis
VIII. Cervical nerve root Pectoralis major Deltoid (clavicular) Pronator teres Palmaris longus Flexor sublimis and profundus Flexor carpi ulnaris	Teres major Latissimus dorsi Serratus magnus All three heads of triceps Extensor radialis Extensor communis Extensor ulnaris Abductor of the thumb Dorsal interossei
I. Dorsal nerve root Pectoralis Deltoid (clavicular) Flexor sublimis and profundus Flexor carpi ulnaris Palmar interossei Lumbricals	Long head of triceps Extensor communis Extensor ulnaris Abductor of thumb Dorsal interossei
II. Dorsal nerve root Palmar interossei Lumbricals	

Forgue also divided certain nerve roots, and kept the animals alive to study the paralysis which would result; but his results were very unsatisfactory, and he could come to no conclusions from them. He attributes his failure to the implication of roots, other than that divided, in inflammatory cicatricial tissue, which led to more extensive paralysis than that due directly to division of any given nerve root.

III. Anatomical Introduction.

The Brachial Plexus in the Dog.—**Ellenberger** and **Baum**[*] describe and figure the brachial plexus in the Dog as found from the four last cervical (V., VI., VII., and

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[*] **Ellenberger** and **Baum**, "Systematische und topographische Anatomie des Hundes," Berlin, 1891, p. 542.

VIII.) and the first and second thoracic nerve roots. The fifth cervical root is said to only send a feeble branch to the phrenic nerve; the sixth forms the suprascapular nerve, and sends a branch to the phrenic; the seventh sends branches to the musculo-cutaneous, phrenic, the median and circumflex, and forms an infrascapular nerve, and an anterior thoracic nerve; the eighth also forms an infrascapular and a thoracic nerve, besides helping in the formation of the musculo-cutaneous, musculo-spiral, circumflex, ulnar, and median nerves. The first dorsal root is said to form the posterior thoracic nerve, and to send branches to the ulnar, median, and radial. With it a feeble branch from the second dorsal root is said to be united. In the diagram of the plexus, a cord connecting the sixth and seventh cervical nerve roots is figured.

CHAUVEAU and ARLOING[*] do not give a separate account of the brachial plexus of the Dog, but describe that of the Carnivora, and mention any special points in which the Dog's plexus departs from the general type. They state that the last four cervical nerve roots and the first dorsal nerve root enter into the formation of the brachial plexus of the Carnivora; but that the twig from the fifth cervical root is an insignificant one. The musculo-cutaneous nerve is said to be formed from the sixth and seventh cervical roots; the musculo-spiral in the Dog exclusively from the eighth root, afterwards receiving branches from the median, ulnar, and circumflex nerves. These authors do not state from which roots the median and ulnar nerves are derived, but mention the fact that the ulnar joins the median in the upper arm, and that the median receives a branch from the musculo-cutaneous just above the elbow joint.

FORGUE[†] describes and figures the brachial plexus of the Dog, as formed by the three last cervical and the first two dorsal nerve roots. In his description he applies the term "médian externe" to what we would call the musculo-cutaneous, which is said to be derived from the sixth and seventh cervical roots. What he calls the "médian interne" we know as the median, and is formed from the eighth cervical and the first dorsal roots, according to him. His radial corresponds to our musculo-spiral, which he states has its origin from the seventh and eighth cervical and the first dorsal nerve roots, while the ulnar is derived from the first dorsal root.

A comparison of these descriptions shows us that certain discrepancies exist in the observations of these authors, for while ELLENBERGER and BAUM describe the musculo-cutaneous nerve as receiving its fibres from the seventh and eighth cervical nerve roots, the other observers quoted describe it as being supplied by the sixth and seventh cervical roots. In like manner the musculo-spiral is said by CHAUVEAU and ARLOING to come from the eighth cervical nerve root exclusively, afterwards receiving branches from certain other nerves; ELLENBERGER and BAUM describe it as having its origin from the eighth cervical and first dorsal roots, while FORGUE adds the seventh cervical root to those already mentioned. The median nerve is formed from the seventh and eighth cervical and the first dorsal nerve roots, according to ELLENBERGER and BAUM, while FORGUE omits the seventh cervical root in his description of the origin of this nerve. ELLENBERGER and BAUM say that the ulnar nerve springs from the eighth cervical and first dorsal roots; FORGUE, on the other hand, describes it as coming solely from the first dorsal nerve root.

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[*] CHAUVEAU, "Anatomie Comparée des Animaux Domestiques," 1871, p. 811.

[†] FORGUE, *loc. cit.*, p. 44.

From numerous careful dissections in the Dog, I find the following arrangement to be the most constant, but variations, of course, occur.

A. *Nerves.*—Only the sixth, seventh, and eighth cervical, and the first, and a minute twig from the second, dorsal nerve roots enter into the formation of the brachial plexus of the Dog (Plate 10, see fig. 1). The twig from the fifth cervical which is mentioned by certain authors, I have been unable to find, and the results of stimulation of this root confirm, at any rate for motor fibres, this anatomical observation, as will be subsequently seen. This root supplies the humero-mastoid muscle and gives a branch to the phrenic, thus supplying the diaphragm.

The musculo-cutaneous nerve at its origin comes exclusively from the seventh cervical and sometimes receives supply from the sixth root by axillary junctions. It sends a branch to the median nerve just above the bend of the elbow. The circumflex nerve is derived from the seventh cervical nerve root. The musculo-spiral takes its origin from the two last cervical and the first dorsal roots, the median from the eighth cervical, and the ulnar from the first dorsal root. The median joins the ulnar in the upper part of its course, and then separates from it again; the junction is one in which the ulnar sends a bundle of fibres to the median, and the median a bundle to the ulnar.

It will be thus seen that my observations, while not absolutely coinciding with those of any individual previous observer, agree in certain points with the observations of all of them.

B. *Muscles.*—The flexor carpi ulnaris muscle derives its nerve supply from both the median and ulnar, thus differing from Man, in whom it derives the whole of its supply from the ulnar. Very little need be said with regard to the other muscles, the majority of those found in the Monkey and Man being more or less perfectly represented in the Dog, but the supinator longus is so rudimentary that it is almost invariably destroyed during the reflection of the skin of the forearm. There is only one muscle representing the two radial extensors of the wrist, but its tendon of insertion divides into two, one half corresponding in its point of insertion to that of the long radial extensor of Man, while the other to that of the short radial extensor.

Although further details of the arrangement of the muscles is not required, it is very necessary to draw attention to certain consequences of their actions. In studying the mechanism by which the movements are brought about at the various joints, I found that action of the deltoid produced, in addition to the movement at the shoulder, a passive extension at the elbow joint. This latter might be produced by the force of gravity, the forearm simply falling as the upper arm is raised; but on the other hand, it can be produced owing to the fact that the long head of the triceps is not long enough to allow the upper arm to be raised to the level of the shoulder without its pulling on the forearm, and thus producing extension at the elbow. A more remarkable effect, however, is that which resulted when traction was directly made on the triceps, for not only was extension at the elbow produced, but extension of the whole extremity including the digits, all the segments of the limb being thus brought into a straight line. The way in which this is produced is that the extensor carpi radialis passes over two joints, viz.: the elbow and wrist, and the muscle is not long enough to allow the elbow to be fully extended without its pulling on the metacarpal bones into which it is inserted, and thus producing extension of the wrist. In like manner, the extension of the toes is due to the fact that their extensors, which also pass over more than one joint, are too short to allow extension at the wrist without their pulling on the bones into which they are inserted.

GAD* relates an exactly similar experience in connection with the posterior extremity of the Frog. He found that by drawing on the ilio-psoas muscle, he produced not only flexion of the thigh on the abdomen, but also of the leg on the thigh, and dorsiflexion of the foot on the leg, in fact the extremity was placed exactly in the position of a frog about to jump. The cause of this was found to be the fact that the insufficient length of the ham-strings did not allow complete flexion at the hip without pulling on the leg, and thus producing flexion at the knee. Then as the tibialis anticus has its origin above the knee joint, dorsiflexion at the ankle followed as a necessary consequence, the tibialis anticus in its turn not being long enough to allow of such extreme flexion at the knee, without drawing on the foot. The importance of these observations becomes apparent when we consider the numerous fallacies which would result if these facts were not borne in mind when we observed the various movements produced by stimulation of any single nerve root. Stimulation of a root, in which extension of the elbow is represented, would also produce extension of the hand and fingers, whether the muscles moving these parts were truly represented in that root or not. If one muscle can directly or indirectly produce movements at so many joints, it is clear that we must first eliminate the indirect effects of the action of this muscle, before we can study the movements of these joints, as produced by the muscles which act directly on them. The omission of this small detail possibly accounts for PANIZZA's conclusion that it was necessary to divide every root supplying an extremity before he could produce complete paralysis of any single movement.

An instrument was devised as follows, by means of which fixation at the elbow joint was obtained, without interfering with the play of the muscles acting on the wrist and digits (Plate 10, see fig. 2). The elbow was first flexed at an angle such as would place the extensors and flexors of the forearm as nearly as possible at an equal advantage. The fixation was next obtained by an instrument consisting of two metal rods, one of which, as shown in the figure, was screwed into the head of the humerus, while the other, which had a clamp at one end, was fixed to one of the bones of the forearm; a rectangular rod was interposed between these rods, and one of its arms fixed to that which was screwed into the humerus, while the other was fixed to that connected with one of the bones of the forearm. These connections were brought about by means of double joints, so that the different rods could be fixed in any position with regard to each other, and thus the angle of the elbow could be varied to almost any degree necessary. The point of fixation of the rod connected with one of the bones of the forearm, was a point an inch to an inch and a half above the wrist joint. When pronation and supination were also to be excluded, this arm of the instrument was attached to the radius, otherwise it was, of course, usually fixed to the ulna. A rod fixed to some part of this instrument served to connect it to an iron upright screwed into the table; fixation being brought about in each instance by means of a double joint. This served to eliminate the movements at the shoulder also, and thus to give a still better opportunity of studying the movements at the wrist and digital joints pure and simple.

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* GAD, "Einige Beziehungen zwischen Nerv, Muskel und Centrum," DU BOIS-REYMOND's Archiv, 1880, p. 568.

IV. Operative Procedure.

Operation.—In every experiment the animal was narcotized with ether, either alone, or in combination with the subcutaneous injection of morphia. The animal was kept deeply under the influence of the narcotic during the whole of the experiment, and killed by an overdose of it at the end, except in the experiments in which the animals were allowed to live for a week or two, for the study of the degenerations which followed the division of nerve roots. In these latter cases the operation, which was always a very trivial one, was done under strict antiseptic precautions, and the small wound afterwards dressed antiseptically. The animals were of course narcotized in these, as in the other class of experiments.

The nerve roots were exposed in the neck, and traced to their points of exit from the intervertebral foramina. Two ligatures were passed round each root, the one as near to the vertebral column as possible, and the other a few millimetres distally from the first, and the root was then divided between the two ligatures. The same number of knots were made on each corresponding pair of ligatures, so that they could be compared when the dissection was made afterwards.

Post-mortem.—In every case a dissection was made so as to exclude the possibility of one nerve root being mistaken for another during the operation. The proximal ligature served a useful purpose, as without it one had to contend with troublesome hæmorrhage from branches of the intervertebral artery accompanying the nerve-root.

Excitation.—The distal portion of the divided root was then raised in the air and stimulated by means of fine platinum electrodes attached to the secondary coil of a du Bois-Reymond's inductorium supplied by a Daniell cell. Exactly the same apparatus was used in excitation of the cortex cerebri (*vide infra*).

V. Division of Subject and Analysis of Results.

A. *Division of the Subject.*

In the following research I naturally approached the question by simple excitation of the peripheral end of the cut root, and the observation of the compound movement thus produced forms the first part of the investigation.

The next step was to carry out, if possible, a minute analysis of this combined movement dividing it into its component factors, *e.g.*, by using minimal currents of excitation applied to the separate bundles of nerve fibres in the nerve root. The strength of current necessary to produce the maximum effect, without diffusing to other nerve roots was found, on the average, to be that in which the secondary was 15 centims. distant from the primary coil. Every care was taken to avoid the possibility of errors from the diffusion of the current to other nerve roots. On using minimum strengths of current, secondary 25 centims. distant from primary coil, on the average, I found first that it was actually possible to obtain different movements by placing the electrodes on different points of the circumference* of the nerve root. I further noticed that on stimulating on one side of one of the small blood-vessels that could be seen with the naked eye running along the surface of the nerve root, a different movement was obtained to that evoked by stimulating the part of the root on the other side of such a vessel. Further, as is well known, the surface of the transverse section of a nerve root presents distinct divisions into bundles. It therefore seemed not unlikely that each bundle of fibres represented a different movement, and that with a little care it might be possible to divide the nerve roots longitudinally, and to separate the different bundles, and thus differentiate the representation of one movement from that of another. Accordingly using the small vessels before mentioned as guides wherever they existed, I divided each nerve root longitudinally into several different bundles, and found that by stimulating each bundle separately a different movement was obtained. These bundles corresponded to the natural bundles of which any given nerve root was composed.

This minute differentiation forms, therefore, the second part of the investigation.

Thus far the investigation dealt with movements. It was obviously necessary to pursue the matter further, and to see upon dissection what individual muscles were innervated by the various roots or their parts when successively excited. This forms the third part of the work. As a corollary to this latter question, I have attempted to determine to what degree any given root supplies a muscle when the latter is innervated from several roots, and whether any given muscle is possibly supplied from more than one root. The instituting new experiments in control of the results obtained by the foregoing methods led to the planning of the following procedures.

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* Beevor and Horsley, 'Roy. Soc. Proc.,' 1888.

Of these, the first, constituting the fourth part of the investigation, consisted in dividing one root, and then seeing what effect was produced thereby in the direction of alteration in the natural gait or movement of the fore-limb in progression.

Another control method, the results of which are embodied in the fifth part, was devised as follows:—A nerve root was divided (in some cases two roots); general epilepsy was then induced by electrical excitation of the cortex, and the resulting deficient participation, in the fit, of the limb in relation with the divided root carefully observed.

Finally, in the sixth part are collected the results of degeneration consequent upon section of the root or roots some time before death.

B. *Analysis of the Results.*

It will be more convenient and instructive to place together the results obtained in Parts I. and II. of the investigation. They are based on a large number of experiments, and, although variations were met with, the results which appeared to be the most constant are those given here.

Part I. Compound Movements obtained by Excitation of the whole Nerve root.
Part II. Minute Differentiation obtained by Excitation of the Individual Bundles of the Nerve root.

Fifth Cervical Root.

No movement whatever of any part of the extremity under observation, with the exception of the scapula being fixed to the trunk, and drawn slightly upwards.

Sixth Cervical Root.

Part I. Upper arm raised to the level of the shoulder, with the forearm at right angles to the upper arm, the limb being adducted to the trunk and the elbow rotated out.

Part II. (1)* Upper arm raised to the level of the shoulder.
(2) Adduction of the arm to the side of the trunk, with outward rotation of the elbow.
(3) Flexion at the elbow.

[* The small numbers in brackets denote each of the individual bundles into which the nerve root was separated. Only those bundles destined for supplying muscles of the extremity are noted, which accounts in part for so few bundles being mentioned in connection with some roots; but it must also be remembered that the roots vary in size, the sixth cervical, and especially the second dorsal, being much smaller than any of the other nerve roots which enter into the formation of the brachial plexus. February 3, 1893.]

Seventh Cervical Root.

Part I. Fore-arm flexed fully on upper arm, the wrist touching the shoulder, and the whole limb drawn across the front of the thorax towards the opposite side.

Part II. (1) Upper arm raised to the level of the shoulder.
(2) Abduction of the elbow from the trunk, with rotation of the elbow inwards, *i.e.*, turning of the fore-arm on to the trunk.
(3) Drawing of the limb across the front of the thorax.
(4) Retraction of the elbow.
(5) Flexion ,, ,,
(6) Extension ,, ,,
(7) Flexion ,, wrist.
(8) Extension ,, ,,
(9) Supination ,, forearm.

Eighth Cervical Root.

Part I. The whole limb extended straight down by the side of the trunk, parallel to its long axis and in a straight line, with the digits very slightly separated.

Part II. (1) Arm drawn to the side of the trunk with tilting of the elbow outwards.
(2) Arm drawn down from the shoulder and fixed to the side.
(3) Arm drawn across the thorax to the opposite side.
(4) Arm drawn to the same side of the thorax.
(5) Retraction of the elbow.
(6) Extension ,, ,,
(7) Flexion ,, wrist.
(8) Extension ,, ,,
(9) Supination ,, forearm.
(10) Pronation ,, ,,
(11) Flexion ,, digits.
(12) Extension ,, ,,

First Dorsal Root.

Part I. The whole limb extended downwards obliquely across the same side of the abdomen, with the forearm pronated, slight ulnar flexion at the wrist, and wide separation of the digits.

Part II. (1) The arm drawn down and fixed to the side of the trunk.
(2) Extension of the elbow.
(3) Pronation of the forearm.
(4) Flexion of the digits.
(5) Extension ,,
(6) Abduction ,,
(7) Adduction ,,

Second Dorsal Root.

Part I. Digits separated and slightly flexed.
Part II. (1) Flexion (interosseal) of the digits.
(2) Abduction of the digits.

Part III. Direct Observation (after Dissection) of Muscles thrown into Action by Excitation of the Separate Nerve Roots.

I next attempted to ascertain, as far as possible, which muscles are thrown into action by stimulation of the several nerve roots. The superficial muscles were exposed by removal of the skin and examined, while, with regard to the deep muscles, I frequently was able to examine them directly after the animal was killed, because the nerve roots at the end of a prolonged experiment retained their excitability for a considerable time, half-an-hour or more.

On account of the fact that no result among the muscles of the fore-limb followed excitation of the fifth cervical root, attention was only paid to the three lower cervical and the two upper dorsal roots with the following results :—

Sixth Cervical Root—

Brachio-mastoid.
Diaphragm.
Deltoid.
Supraspinatus.
Infraspinatus.
Subscapularis.
Coraco-brachialis.
Biceps.
Brachialis anticus.

Seventh Cervical Root—

Diaphragm.
Deltoid.
Supraspinatus.
Infraspinatus.
Subscapularis.
Teres.
Coraco-brachialis.
Biceps.
Brachialis anticus.
Triceps.
Flexors of the wrist.
Extensors of the wrist.
Supinator brevis.
Pectoralis.
Serratus magnus.

Eighth Cervical Root—

Pectoralis.
Teres.
Latissimus dorsi.
Triceps.
Flexors of the wrist.
Extensors of the wrist.
Supinator brevis.
Pronator teres.
Flexors of the digits.
Extensors of the digits.

First Dorsal Root—

Latissimus dorsi.
Triceps.
Pronator teres.
Flexors of the digits.
Extensors of the digits.
Interossei.

Second Dorsal Root—

Intrinsic muscles of the paw.

It is interesting to notice that, on the whole, the results obtained by me correspond to those obtained by FORGUE with a few exceptions, to which it may be well to call attention. With regard to the muscles supplied by the sixth root, there is only one point of difference. I find that the deltoid is supplied by this root, but FORGUE does not. The seventh root supplies the supinator brevis according to my observations, and not the latissimus dorsi and pronator teres as found by FORGUE, while he does not mention the supply of the supinator brevis at all in connection with any of the roots. The chief points of difference as to the muscles supplied by the eighth cervical root are that I do not find the deltoid and interossei thus supplied, while FORGUE does; and he does not mention the supinator brevis, while I find it to be supplied by this root. The representation of the deltoid and the omission of the pronator teres by FORGUE are the only points on which we differ with regard to the muscles deriving their nerve supply from the first dorsal root; and we are at one as to those muscles which depend on the second dorsal root for a like supply. Possibly the points of difference between FORGUE'S observations and my own are not so numerous as would appear from what has just been said, as his schematic representation, in order to show that each nerve root supplies muscles on both the anterior and posterior surface of the limb leads to slight confusion as to whether certain of the muscles are meant to be represented in certain roots; notably is this the case with regard to the deltoid, which I find it difficult to imagine as represented in the eighth cervical, much less the first dorsal nerve root.

Corollary to Part III.—The question which next arose for consideration was whether or no a single bundle of fibres representing a single simple movement ever remains distinct in a nerve root during its course to the muscles it supplies without inosculating with other nerve fibres. That each bundle does remain distinct is, I think, proved by the following facts:—

(*a.*) If a bundle of nerve fibres is separated in a nerve root, it can, in the Dog, be followed by dissection through the plexus and along the course of the nerve in which it runs, to its termination either in a muscle or in the skin.*

(*b.*) If a bundle thus isolated in a nerve root be stimulated a simple movement results and not merely the combined movement in only a lessened degree proportional to the diminished number of nerve fibres stimulated.

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* *Cf.* HERRINGHAM, PATERSON, &c., *loc. cit.*

(*c.*) If a minimal stimulus be used one can localize different movements in different parts of the circumference of the peripheral nerve just as has been shown above to be possible in exciting a nerve root.

(*d.*) If the musculo-cutaneous be divided below the point where it gives off the twig to the median, and if the trunk of the nerve, above the point where the twig is given off, be stimulated, the pronator radii teres muscle contracts, and it alone. At first I was under the impression that the extensor carpi radialis was the muscle that contracted, but more careful separation of the two muscles by dissection showed that the movement in the latter muscle was due to traction on it owing to its connections with the adjacent pronator.

(*e.*) If a root be divided the degeneration which results in the various nerves receiving fibres from the root is not scattered but is limited to distinct strands sharply defined.

A further point to be determined in this connection was the question whether when a muscle receives nerve fibres from more than one cervical brachial nerve root, both nerve roots supply fibres to one and the same muscle fibre. The muscle chosen for these observations was the flexor carpi ulnaris, which, as we have already seen, is supplied both by the median and the ulnar trunks in the Dog. Now when the eighth cervical or first dorsal nerve root was stimulated alone, with a strong current, the maximum contraction of the flexor carpi ulnaris obtained was considerably less than that produced by stimulating both roots simultaneously. From this experiment it follows that the muscle fibres which are supplied by nerve fibres from one root in all probability do not receive nerve fibres from any other. This view is further supported by the experiment of GAD* on the lumbo-sacral roots of the Frog; for he showed that when a muscle is supplied by two nerve roots simultaneous stimulation of both roots produced an effect in the muscle equal to the sum of the contractions produced by stimulation of each root separately.

Part IV. (Control). Alteration in the Action of the Fore-limb in Progression or in Standing evoked by Section of a Nerve Root.

The following experiments were performed to observe the effect of division of a nerve root on the movements by the limb during use in ordinary progression, &c. The four last cervical and the first dorsal nerve roots were each in turn divided in different animals under antiseptic precautions and a portion removed to prevent the possibility of reunion.

All the wounds healed by primary union except in one instance, and subsequent dissection in each case proved that none of the other roots were implicated in any of the cicatricial tissue. Each animal was kept under observation for a fortnight and then killed.

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* GAD, *loc. cit.*

After division of the fifth nerve root alone absolutely no alteration could be observed in the mode of progression of the animal.

Division of the sixth root was followed by distinct paresis of the corresponding extremity, evidently chiefly implicating the muscles about the shoulder, the elbow tending to rotate away from the trunk when the animal walked; if the other fore leg were passively raised off the ground, the Dog had some difficulty in supporting the weight of the body on the leg, the nerve root of which had been divided, and in some cases failed to do so. In this as well as in the case of all the other nerve roots divided, this effect was most marked during the first twenty-four hours, after which it quickly passed off, so that in a day or two very little abnormality was noticeable, and by the end of a week it was difficult to say that there was any difference on the two sides. The effect of division of the seventh root resulted in a more extensive paresis, as it was evident that besides the slight tendency for the elbow to rotate away from the trunk on that side, there was some interference with the motor power of the lower segments of the limb, which made the lameness more noticeable than in the last instance. The most pronounced effect was that which followed division of the eighth cervical root, which is considerably the largest which enters into the formation of the brachial plexus in the Dog, the paresis being especially marked about the wrist, and the animal walking with a slightly high stepping action on the side of the divided root. Very little effect was produced by division of the first dorsal root, the resulting lameness being exceedingly slight and passing off very rapidly.

That reunion of the divided ends of the nerve roots was not the cause of the improvement in motor power which took place in each instance is proved by the fact that on post-mortem examination there was not the slightest sign of such reunion. Further, microscopic examination showed well-marked degeneration, both in the distal end of the roots divided, and in the nerves derived from these roots. As has already been shown, a muscle which obtains its nerve supply from several roots has some of its fibres innervated from one, while the remainder are innervated from another or other roots, so that the recovery cannot be explained by supposing that the same number of fibres are acted on as before, and that they gradually become accustomed to respond more powerfully to the stimulus, although that is necessarily less intense. At the end of three weeks the muscles supplied by the divided root were found to be considerably atrophied and softer than normal; and there was marked diminution of resistance when passive movements were carried out at these various joints on which these muscles acted. Moreover, during general epileptic convulsions artificially induced, these muscles did not stand out nearly so vigorously as did those on the non-affected side.

Division of the nerve root so near to the spinal cord may be supposed to have produced an amount of shock sufficient to render that part of the cord functionally inactive, or rather, reduced in its power of conduction. But if this were the case, there would at least have been some sign of weakness in the opposite fore leg, and probably also in the hind legs.

The only other explanation which suggests itself to my mind as possible is one or other of the following. Possibly certain cortical cells give origin to fibres which run in different roots to the same muscle or others of similar function, and division of one of these nerve roots produces a reflex inhibitory effect* on the cortical cells from which its fibres are derived, so that the original motor paralysis is more pronounced than that actually depending on the cutting off of the impulses which formerly travelled along the root that is now divided; and that as the cortical cells recover from this inhibitory effect, so the motor power is restored up to a certain point, the residuum not recovered from depending directly on the loss of the impulses which formerly reached the muscles through the now divided root. On the other hand, it may be that the cortical cells are capable of discharging the same amount of energy as formerly, but that the impulses meet with a block owing to the division of the fibres along which they formerly passed. Gradually, however, the impulses are diverted, it may be through the anterior horn cells of the spinal cord along other channels, and thus in time the fibres of the muscle which are supplied by an intact root receive almost the same amount of stimulation as did the whole muscle formerly.

It is worthy of note that FORGUE could come to no satisfactory conclusions from the results which he obtained by this method of experimentation. He always found that the amount of motor enfeeblement was out of all proportion to that which could possibly be produced by division of a single nerve root; and on examination he invariably found that nerve roots other than that divided were implicated in the mass of inflammatory cicatricial tissue which resulted as a consequence of the suppuration of the wounds, a complication which never gave any trouble in the present research, as all of the wounds healed by primary union except in one case.

Part V. (Control). Influence of Section of Root or Roots in excluding part of an Epileptic Spasm induced in the Limb by Cortical Excitation.

In my next series of experiments I tried to see what information could be obtained as to the functional relations of the nerve roots to the muscles they supply, by the following method of experimentation:—A nerve root was first exposed, but not divided; the cranium was then opened *lege artis* over the excitable area on the same side as the exposed nerve root, in order to avoid the possibility of injuring the cortical centres (*i.e.*, opposite) corresponding to the limb deriving its supply from that root. General (*i.e.*, bilateral) epilepsy was then produced by stimulation of the exposed cortex with the induced current as above stated, and the positions of the two fore extremities were seen to be identical during the fit. The exposed root was next divided, general epilepsy again produced, and the positions of the two fore extremities once more compared. The position assumed by the two fore extremities before interference with the root, and of the sound one after the root on the other was divided, was as follows:—In this case, *i.e.*, the normal condition, the elbow was drawn close to the side of the thorax, the fore-arm held at right angles to the upper arm, and projected straight forward by the side of the thorax, the fore-arm, wrist, and fingers being in a straight line. During the first stage of the seizure, *i.e.*, during the tonic spasm, the extremity was raised parallel to the neck, with the paw on a level with the side of the head.

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* *Cf.* BUBNOFF and HEIDENHAIN, 'PFLÜGER'S Archiv.'

If, now, the sixth cervical root were divided, the elbow, during the epileptic convulsions, projected from the side of the trunk notably more than on the sound side, and the forearm was thus inclined across the trunk somewhat, so as to form an acute angle with the side of the thorax. It (the fore-arm) was still held at right angles to the upper arm, and the fore-arm, wrist, and fingers were, as before, in a straight line. During the tonic stage, the extremity was never raised higher than the level of the shoulder. This experiment shows, in a striking manner, that the exclusion from the fit of the muscles supplied by the sixth cervical root, means a loss of the same movements (*i.e.*, chiefly shoulder) as those previously determined by direct excitation of the root itself.

After division of the seventh cervical root, the elbow was fixed closer to the side of the thorax than on the normal side, the fore-arm extended obliquely across the abdomen, this demonstrating clearly the exclusion chiefly of the flexors of the elbow. (See p. 52).

Similarly division of the eighth cervical root alone was, in contrast to what has just been said, attended by elevation of the shoulder and noteworthy flexion at the elbow during the epileptic convulsions. Moreover, flexion of the paw at the wrist and of the digits predominated over extension. During the epileptic convulsions that were produced in a fourth animal, after the first dorsal root had been divided the upper arm remained close to the side of the trunk, in the same position as on the unaffected side, but the fore-arm became strongly flexed at the elbow (*i.e.*, owing to exclusion of triceps extension), so as to be parallel with the side of the neck. The fore-arm and wrist were in a straight line, but the digits were flexed and adducted.

I next performed in different animals combined section of more than one root as follows:—

The sixth and seventh cervical roots were simultaneously divided on the same side. During the convulsions the whole extremity was strongly extended down the side of the abdomen, the wrist and digits slightly curved in flexion, and the digits separated.

When in another animal the seventh and eighth cervical roots on the same side were similarly divided, the arm was a little more raised at the shoulder than on the opposite intact side, the fore-arm flexed on the upper arm, but not nearly so strongly as when the eighth root alone was divided.* The paw was flexed at right angles to the fore-arm at the wrist, and the digits interosseally flexed in the characteristic claw-shaped position, viz., hyperextension of the first phalanx with flexion of the distal phalanx. In the next experiment the eighth cervical and first dorsal roots were severed on the same side. On evoking the generalized convulsions the fore-arm was strongly flexed on the upper arm, as when the first dorsal alone was cut. Marked tendency to drop wrist, owing to very feeble spasm of the extensor muscles, was noted, and the digits were but slightly adducted and fully flexed.

In the next case the sixth, seventh, and eighth cervical roots were divided on the same side, and in the fit the elbow was fully extended as in unopposed triceps action, and the digits were spasmodically fixed in the claw-shaped position.

The fifth cervical root was then divided in addition to the three just mentioned; but the position of the limb, during the epileptic convulsions, was not altered by this, confirming the statement made on p. 47 that the fifth cervical root takes no share in the motor representation of the plexus. When the seventh and eighth cervical and the first dorsal nerve roots were divided the limb was extended straight forward from the shoulder, the whole extremity being in a straight line projecting in front of the animal and not raised above the level of the shoulder. Finally all the nerve roots entering into the formation of the brachial plexus were then divided. During the epileptic convulsions the extremity under these circumstances remained intrinsically motionless, although the limb was passively shaken by the convulsive spasms of the rest of the body.

So far as I am aware, this is the first time that this method of experimentation in connection with the nerve roots has been employed. It will be well, therefore, to point out that it possesses the double advantage of being a means of checking the results of direct stimulation experiments, and affording us the power of ascertaining whether elimination of a root does or does not result in incoordination of the remaining combination of movements. A few moments consideration shows that the results of these experiments completely confirm those obtained by stimulating the individual nerve roots, for during an epileptic fit, when a nerve root is cut, the muscles that act feebly are only those which are brought into action by direct stimulation of the same nerve root. Further, we see that the impulses travelling along the undivided roots produce perfectly coordinated movements, so that the coordination of the movement produced by the remaining roots is not in the slightest degree affected by the elimination of any one of them. These experiments also make it clear that when the section of the root and the cortical excitation are made at the same time there cannot be overflow of nerve impulses through the spinal centres, at any rate to any great extent. That is to say, impulses which should reach the muscles through the nerve root that has been divided, do not under these circumstances reach them by other commissural channels.

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* Because of course the seventh cervical root has also been divided. See p. 58.

Part VI. (Control). Differentiation of Parts of the Nerve Roots by the Degeneration Method.

The last set of experiments which were performed may, for convenience, be termed degeneration experiments. In these certain nerve roots were divided under the influence of an anæsthetic, and with antiseptic precautions. The animal was in each instance allowed to live for three weeks, and then killed. In order to prevent tedious repetition, it will suffice to say that microscopic examination showed that these experiments confirmed the anatomical facts that had been previously ascertained, as degeneration following section of a root was found only in those nerves which had been shown to have their origin from it. For example, division of the sixth root was followed by degeneration in the musculo-cutaneous, thus proving that this nerve does receive fibres from the sixth root in some cases; so, too, the musculo-spiral, about the origin of which there are discrepancies in the statements of different observers, was found to have some of its fibres degenerated after division of the seventh root. Another point of interest in connection with this root was the degeneration found in the *median* nerve after division of the root in question. It will be remembered that stimulation of the seventh root produced contraction of the pronator radii teres muscle, and that it has been also shown that stimulation of the branch which the musculo-cutaneous nerve gives to the median just above the bend of the elbow results in contraction of that muscle, and it alone.

But, in addition to these facts confirmatory of the results obtained by stimulation, certain interesting points were observed, of which, however, I will only allude to one in the present paper.

According to the Wallerian law of degeneration, division of a nerve root immediately on the distal side of the intervertebral ganglion results in degeneration of its peripheral end, and of that alone, there being no degeneration of the proximal end. In addition to degeneration of the distal end, as the Wallerian law affirms, I found some degenerated fibres in the sensory root between the ganglion and the spinal cord, which points to the probability that there are some fibres which run through the intervertebral ganglion, without being connected with the cells of the same. These observations confirm the statements of JOSEPH,[*] whose experiments of division of the root between the ganglion and the cord showed the existence of such fibres, and which, therefore, must have their trophic centres elsewhere—in the cord. As in my experiments the roots were divided on the distal side of the ganglia, if the trophic centres for these fibres be situated in the spinal cord, the only way in which the explanation will hold good is by supposing that such fibres are recurrent, as CLAUDE BERNARD has suggested, and that they loop back in the plexus, at the junction of the motor and sensory roots.[†] The only other way that the degeneration of these fibres can be explained is by supposing that certain fibres derive their trophic supply in some way from the periphery; but I know of no facts that support any such supposition.

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[*] 'Archiv für Physiol.,' 1887, p. 296.

[†] That this latter position is not the case is proved by my observations.

VI. Summary and Conclusion.

From the results of the various methods of experimentation already detailed, I feel that I am justified in coming to the following conclusions :—

1. *Stimulation Experiments.*

1. The compound movement obtained by stimulation of a whole nerve root is a well coordinated one, depending on the action of a group of muscles in synergic combination, as FERRIER and YEO* showed to be the case in the Monkey.

2. This compound effect may be resolved into its component factors, when it is found that movements diametrically opposed to each other may be represented in the same nerve root, *e.g.*, flexion and extension.

3. Such single simple movements bear an almost constant relation to the nerve roots, the same movements being as a rule found in any given root, and such movements always bear the same relation to the spinal level, *e.g.*, flexion of the elbow is always represented one root higher than extension of the same joint.

4. Fibres representing a certain movement as a rule preserve the same position in a given nerve root, *e.g.*, extension of the wrist is represented by a bundle of fibres in the upper part of the circumference, while flexion is represented by a bundle of fibres in the lower part of the same root.

5. Each bundle of nerve fibres, representing a single simple movement in a nerve root, remains distinct in its course to the muscle or muscles producing such a movement, without inosculating with other motor nerve fibres.

6. The group of muscles supplied by any given nerve root occupy both the anterior and posterior surfaces of the limb,† in other words, muscles whose unimpeded action would produce one movement, are represented in the same root as others whose action would produce a movement diametrically opposite.

7. In such combinations, certain muscles are always more extensively represented than others, so that with a current sufficiently strong to stimulate all the fibres in a nerve root equally, certain muscles predominate in their action over others.

8. The muscles whose action predominates in one root, always predominate in that root.

9. If the muscles producing flexion of a certain joint predominate in their action in one root, those producing extension predominate in another.

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* *Loc. cit.*

† *Cf.* PATTERSON, FORGUE, *&c.*, *loc. cit.*

10. It is possible by stimulation of a single bundle of fibres in a nerve root, to produce contraction of a single muscle and it alone.

11. The same muscle is always represented in more than one nerve root, usually two, and to an unequal extent in these.

12. When the same muscle is represented in two nerve roots, the muscle fibres innervated by one root are not innervated by the other.

2. *Ablation Experiments.*

1. Division of any given nerve root produces paresis of the group of muscles supplied by it.

2. This paresis is only temporary, and soon passes off almost completely.

3. Such division of a nerve root does not result in incoordination of the remaining muscular combinations represented in other nerve roots.

3. *Exclusion of a certain Root or Roots during an Epileptic Spasm in the Limb (the Root being divided at the time, and not some time previously.)*

1. Division of one or more nerve roots produces alteration of the position of a limb during an epileptic spasm, which altered position depends on the particular muscular combinations that have been thus thrown out of action.

2. No incoordination is produced in the action of the remaining muscular combinations.

3. There is no evidence of overflow of the impulses which ought to travel down the divided root, into other channels through the spinal centres so as to reach the muscles by new paths.

4. *Degeneration Method.*

1. These experiments confirm the anatomical facts that had been previously ascertained by dissection, as to which nerve roots supply any given nerve with fibres.

2. The degeneration which results in the nerves is not a scattered one, but is localized to distinct bundles of nerve fibres occupying a certain position in the transverse section of the nerve.

3. The Wallerian law of degeneration, so far as it is applied to the nerve roots and their intervertebral ganglia, is found to be erroneous, for when a nerve root is divided on the distal side of the intervertebral ganglion not only is degeneration found in the peripheral end of such a root, but also in that portion of the sensory root between the ganglion and the spinal cord; pointing to the probability that there are certain nerve fibres which do not depend on the ganglion for their trophic supply, but

derive the same from elsewhere, either the spinal cord at another level, or the periphery.

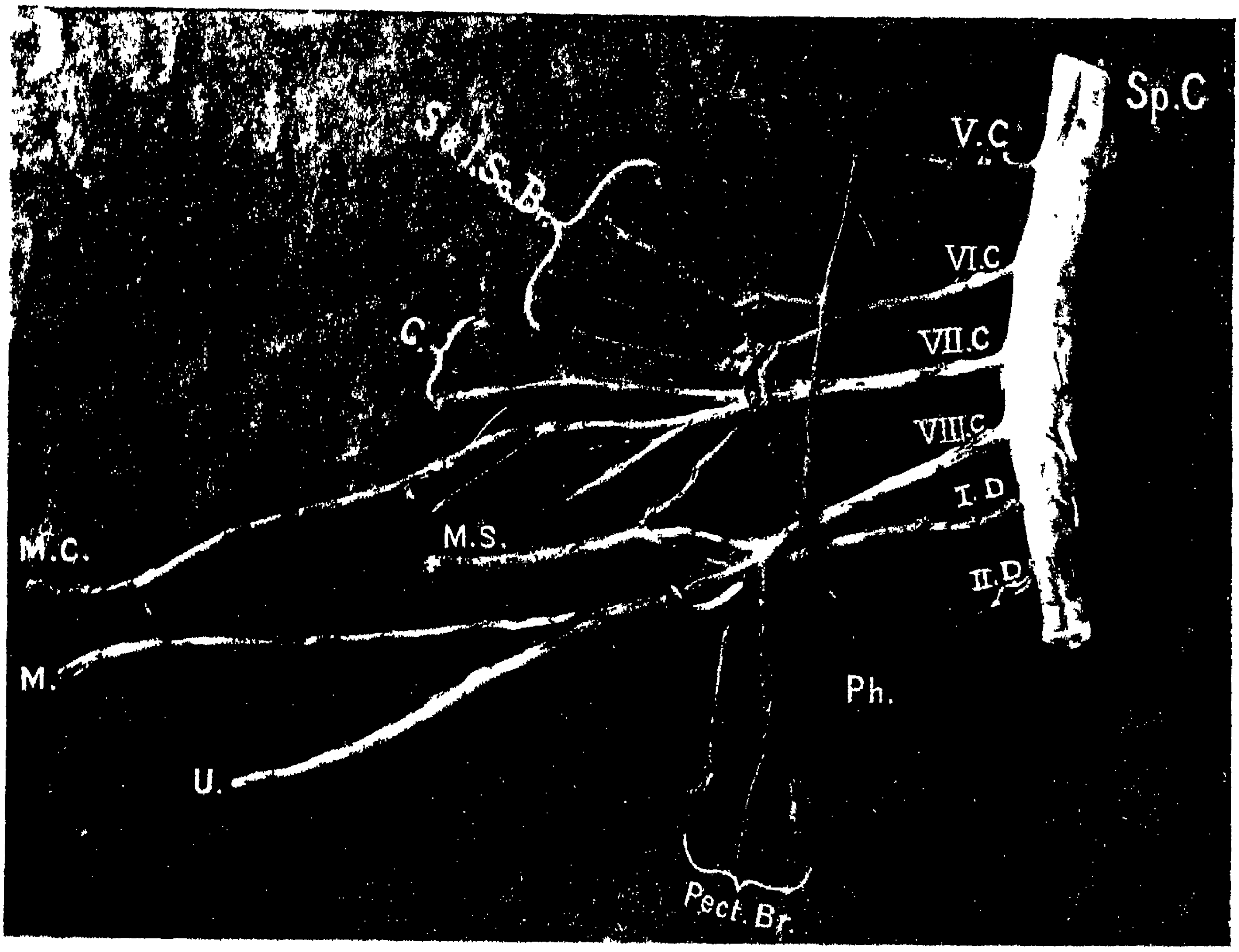
In conclusion I wish to call special attention to the value of the method of excluding one or more nerve roots during an epileptic spasm, as affording us a means of confirming the facts that have been previously observed from stimulation of the nerve roots, and also of ascertaining new facts with regard to them and the plexuses which they form. It supplies us with a valuable means of studying the manner in which conduction of impulses from the cortex through the nerve roots and plexuses to the muscles takes place. Further, the method is capable of still wider extension; as if instead of producing general epilepsy, we apply less powerful stimuli to the centres for different movements, as represented in the motor cortex, we shall be able to connect such centres or parts of these with the nerve roots to which fibres proceed from these cortical motor centres.

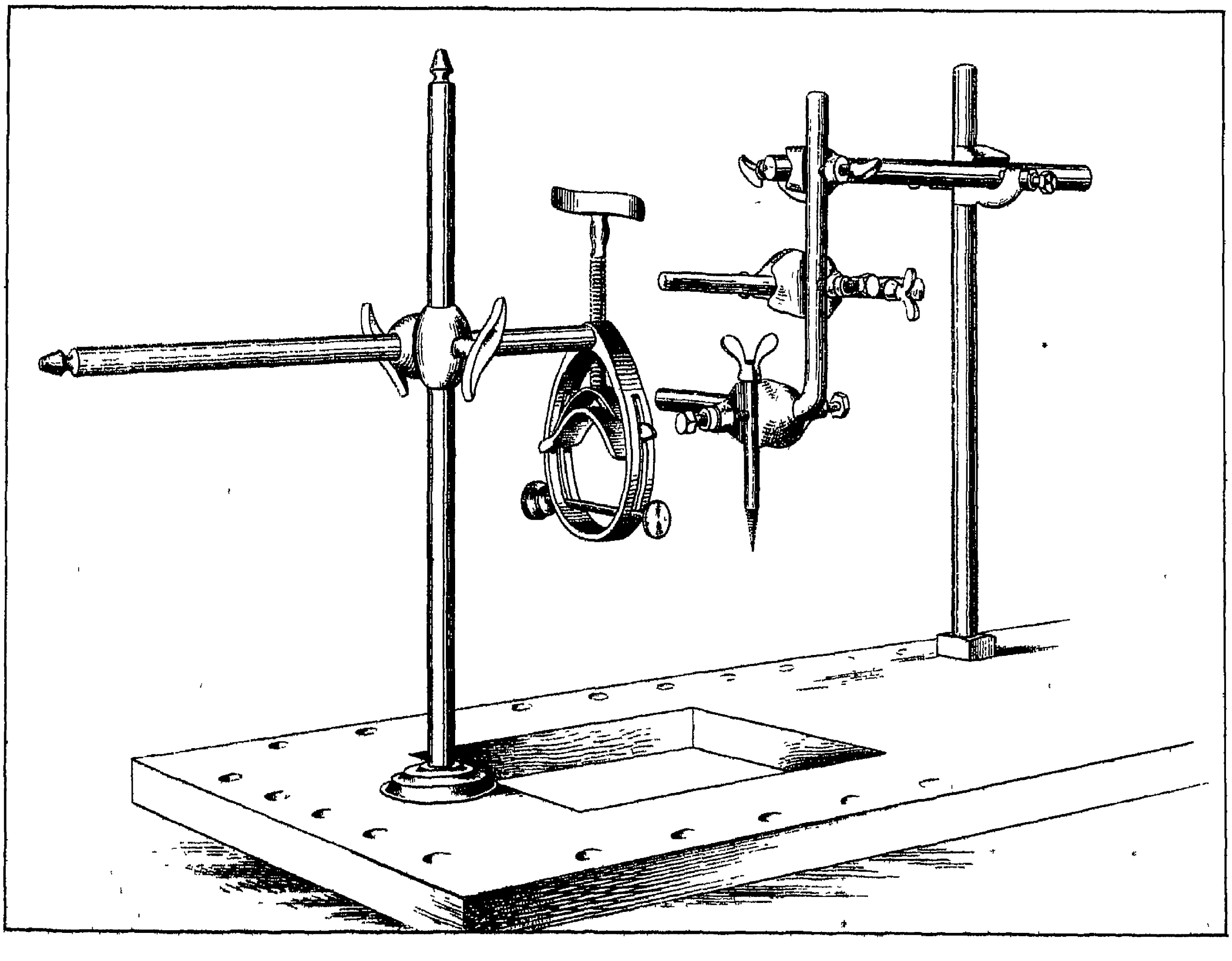
DESCRIPTION OF PLATE 10.

Fig. 1.—This figure is from a photograph of the brachial plexus of the Dog, and shows a portion of the cervico-dorsal cord, the nerve-roots which spring from one side of it, and the nerve trunks derived from these nerve roots.

Sp. C. = Spinal cord.
V.C.
VI.C.
VII.C.
VIII.C. } Represent the fifth, sixth, seventh, and eighth cervical nerve roots.
I.D.
II.D. } Represent the first and second dorsal nerve roots.
Ph. = Phrenic nerve.
S. and *I.Sc.Br.* = Supra- and infra-scapular nerves.
C. = Circumflex nerves.
M.S. = Musculo-spiral nerve.
M.C. = Musculo-cutaneous nerve.
M. = Median nerve.
U. = Ulnar nerve.
Pect.Br. = Pectoral branches.

Fig. 2.—This figure is from a photograph of the instrument which was devised to control the movements at the shoulder and elbow joints when those at the wrist and digital joints were being studied. The instrument proper is to the right in the figure, while that to the left is the ordinary instrument which is used to fix the animal's head in most experiments.





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III. *Contributions to the Anatomy of Fishes.—II. The Air-bladder and Weberian Ossicles in the Siluroid Fishes.*

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Communicated by Professor Alfred Newton, *F.R.S.*

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[Plates 11–19.]

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I. Introductory.

Weber, in his classical memoir entitled "De aure et auditu Hominis et Animalium, Pars i., De aure Animalium aquatilium," published in 1820, was the first to show that in certain families of Physostomous Teleostei, viz., the Siluridæ and Cyprinidæ, there exists a peculiar connection between the auditory organ and the air-bladder, by means of a chain of movably interconnected ossicles. To these two families, and to three others, viz., the Characinidæ, Gymnotidæ, and Gymnarchidæ, in which this singular mechanism was subsequently discovered, Sagemehl (33) applied the collective name of Ostariophyseæ (οσταριον, ossicle; φυση, air-bladder), for the reason that the possession of this highly specialized mechanism implied community of descent. Since the publication of Weber's memoir, various contributions to this subject have been made, but deal for the most part either with special features, or with individual species, or with a very limited number of species in particular families. In no single family of Ostariophyseæ has any attempt at present been made to institute a systematic and comparative examination of any considerable number of genera, and, at the same time, to deal with the various modifications which pertain to the air-bladder, auditory organ, and skeleton as correlated and mutually dependent factors. With regard to papers on such special points as the nature of the "complex" vertebra and the homologies of the Weberian ossicles, reference may be made to the contributions of BAUDELOT (1), GRASSI (17), and NUSBAUM (29), and to a recently published and valuable paper by SÖRENSEN (37), which treats of certain skeletal modifications, not only in the Ostariophyseæ in general but in other Teleostei. Of papers dealing with other special points, the contributions of HASSE (19) and NUSBAUM (*loc. cit.*) to the anatomy of the auditory organ must also be mentioned. Of individual families, the Siluridæ have received but little attention. SAGEMEHL'S paper deals mainly with the air-bladder of the Characinidæ. The papers of GRASSI, BAUDELOT, and NUSBAUM relate almost exclusively to the Cyprinidæ. The valuable observations of SÖRENSEN, while more extensive as regards the families included within the range of his investigations, are nevertheless restricted to certain special features, and, apart from the development of ossifications in its walls, have but scanty reference to the air-bladder, or to the Weberian ossicles, or to the auditory organ in the relatively few Siluridæ described by him. WEBER (*loc. cit.*) himself only described the air-bladder and the ossicles which bear his name in a single species (*Silurus glanis*). JOHANNES MÜLLER, in his various contributions to the Berlin Academy during the years 1843–45, added somewhat to our knowledge of these structures, and notably by his discovery of the "elastic-spring" apparatus, but MÜLLER'S attention was mainly directed to the grosser features in the anatomy of the air-bladder, to the entire exclusion of all but the slightest reference to the important skeletal modifications which are associated with the peculiar structure of that organ in the Siluridæ, or to the auditory ossicles. REISSNER (32) has given a fairly complete account of the singular bone-encapsuled air-bladder of *Rhinelepis*, but among the most valuable of recent contributions to this branch of vertebrate morphology are the papers by Professor RAMSAY WRIGHT relating to the aberrant Siluroid *Hypophthalmus* (44), and to the more normal North American species *Amiurus catus* (42, 43), to which reference will subsequently be made. In this connexion reference may also be made to the numerous scattered references to the air-bladder of the Indian Siluridæ contained in the papers of the late Dr. FRANCIS DAY (9, 10), which, although often too brief, in several instances at any rate are valuable as throwing some light on the degenerate condition of that organ in certain rare abnormal forms.

It is remarkable that this important family of Fishes has so little occupied the attention of morphologists, especially when we take into consideration the interesting modifications which its various members have undergone, and the fact that in this family the air-bladder and "auditory" ossicles are subject to greater variations, and are more thoroughly specialized than in any other group of Ostariophyseæ. Probably the main reason why the Siluridæ have been so much neglected is due to the fact that they are principally tropical in habitat, or live in remote and inaccessible districts. Investigators at home are consequently dependent upon the exertions of collectors, who, as a rule, do not pay much attention to Fishes, and the relatively few species which do find their way to Europe are required for museum specimens. Fortunately for us we had the opportunity of purchasing the third series of the Siluroids collected by that eminent ichthyologist, the late Dr. BLEEKER, who had amassed a magnificent collection of East Indian Fishes, amongst which the Siluridæ were well represented. Subsequently we added to our collection what other specimens we were able to procure, especially African and South American species.

The object of the present communication is to give the results of a detailed study of the morphology of the air-bladder, and "auditory" ossicles, and the associated skeletal modifications in 100 species of Siluridæ, referable to 51 genera, and mainly belonging to Dr. GÜNTHER'S sub-families of Siluridæ Homalopteræ, S. Heteropteræ, S. Proteropteræ, and S. Proteropodes.* Most of the species examined and described by us have either not been the subject of any recorded observations, or the accounts already given are too brief to be of much value; in the few cases in which it is otherwise, references are given to what has previously been recorded.

The physiological significance of the so-called auditory ossicles is still an unsettled problem, and one of the objects of our investigations was to ascertain how far the morphological variations of the mechanism, and of the air-bladder and auditory organ, in a large series of forms were able to throw any light on this difficult question, and failing a satisfactory solution by such means, we shall be satisfied if our results are regarded as furnishing the experimental physiologist with a sufficiently wide and accurate basis of morphological data.

To our friend the late Dr. FRANCIS DAY, of Cheltenham, we are greatly indebted for the gift of numerous valuable specimens and for his kindness in identifying others. We greatly regret that he is not now living to receive this acknowledgment of our gratitude for his liberality and interest in our work. We are also indebted to Dr. GÜNTHER for the acquisition of one or two species, and for his courtesy in allowing us every facility in examining the collection committed to his care; and also to Dr. SIDNEY LAWRENCE, of Birmingham, for a small but valuable series of South American Siluroids collected by himself. We desire also to take this opportunity of thanking Professor J. H. POYNTING, F.R.S., and Dr. W. W. J. NICOL, of the Mason College, for information and valuable criticism on certain physical points, and the Council of the Royal Society for grants to one of us from the Government Research Fund in aid of these investigations.†

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* A preliminary abstract of this paper appeared in 'Roy. Soc. Proc.,' vol. 46, 1889. We may add as a personal explanation that this investigation was commenced by us several years ago, but for various unavoidable circumstances it had repeatedly to be laid on one side.

† The figures illustrating this Paper were drawn from nature by our draughtsman, Mr. HENRY BARNES, of Birmingham.

II. HISTORICAL.

It is unnecessary for us to say anything under this head. Excellent historical summaries of the various views that have been held by different writers as to the modifications of the anterior vertebræ and the homologies of the "auditory" ossicles in the Ostariophyseæ generally, are to be found in the papers of BAUDELOT (1) and SÖRENSEN (37).

III. MORPHOLOGY.

In describing the morphology of the air-bladder and Weberian ossicles, and the nature of the modifications which the anterior vertebræ undergo in the various species of Siluridæ that we have had the opportunity of examining, we propose to follow the system of classification adopted by Dr. GÜNTHER in the British Museum Catalogue of this family (15) and to deal with the different species under the principal subdivisions to which they are referred in that work, commencing however with the sub-family Siluridæ Proteropteræ. A comparison of the species enumerated in the Catalogue with those described in our paper will to some extent indicate the range of our investigations. As we have followed Dr. GÜNTHER in the specific names, we have omitted the authorities for them in the text, but, in the few instances in which the species are not referred to in his Catalogue, the authority is given either in the text or in the index of species.

SUB-FAMILY :—SILURIDÆ PROTEROPTERÆ.

GROUP :—BAGRINA.

Macrones nemurus.

We select for detailed description, in the first place, the Javan species *Macrones nemurus.*

The Vertebral Column.—In this species certain of the anterior vertebræ, from the second to the seventh inclusive, are rigidly connected with one another, partly by the anchylosis of more or fewer of their centra, neural arches, and spinous processes, and partly, also, through the investment of the lateral surfaces of their centra by a continuous deposit of superficial bone. With the exception of those belonging to the second, third, and fourth vertebræ the distinctness of the different vertebral elements is, however, always more or less clearly indicated by the existence of well-marked intervertebral spaces between the centra, which are very obvious in a vertical longitudinal section of this region of the vertebral column, and by the presence of sutures between certain of the confluent neural arches. The neural spines, on the other hand (with the exception of those belonging to the third and fourth vertebræ which are fused, and the spine of the second vertebra which is absent), are distinct, although, for the most part, they are firmly united together, but only by suture. Not only are the anterior vertebræ inflexibly united together, but their connection with the skull is of an equally rigid character, and this is due to the firm articulation of the transverse processes of the fourth vertebra with the skull through the intervention of the post-temporal bones, to the articulation of the arch and spine of the third vertebra with the exoccipitals and supraoccipital, and to the development of strong, interlocking accessory articular processes on the basioccipital and the centra of the first and complex vertebræ.

We defer for the present any reference to the "auditory ossicles" as constituent elements of certain of the anterior vertebræ beyond remarking that in all probability the claustra and stapedes of WEBER respectively represent the neural spine and arch of the first vertebra, while the ossicles, termed incus and malleus by the same morphologist, respectively correspond to the arch of the second vertebra and the transverse process or rib of the third vertebra.

The centrum of the first vertebra (figs. 1, 2, 4, and 5, *v.'*) is much smaller than any of the normal anterior vertebral centra, being represented by a thin discoidal and but slightly biconcave bone, wedged in between the concave posterior face of the basioccipital and the concave anterior face of the complex centrum. Its ventral surface is furnished with a pair of accessory articular processes which fit in between similar but much stronger paired processes developed from the ventral margin of the anterior extremity of the complex centrum, and also from the ventral surface of the posterior end of the basioccipital (figs. 4 and 5, *ac., p.*). On the dorsal surface of the centrum, near its lateral margins, there are two small cup-shaped sockets for the reception of the rounded condylar processes of the two "stapedes." The centrum is quite distinct from the basioccipital and complex centrum, although rigidly articulated to both.

The large vertebra which succeeds the first was regarded by WEBER (*loc. cit.*) as the second. BAUDELOT (1), GRASSI (17), and NUSBAUM (29), however, subsequently showed that in the Cyprinidæ the apparent second vertebra is really formed by the complete coalescence of the centrum of the second vertebra with that of the third; and a precisely similar fusion was believed by them to have formed the "second" vertebra of WEBER in the Siluridæ; but more recently RAMSAY WRIGHT (42, 43) has demonstrated on developmental grounds that, in the latter family, this vertebra is even more complex, inasmuch as it represents, not only the elements already recognised by previous writers, but also, in addition, the centrum, arch, and spine of the fourth vertebra—or, in other words, the "second" vertebra of WEBER is formed by the complete coalescence of the third and fourth vertebræ with each other and with the centrum of the second. From RAMSAY WRIGHT'S account of the development of the anterior vertebræ in the North American Siluroid *Amiurus catus*, it would appear that the usual intervertebral growth of the notochord does not take place between the centra of the third and fourth vertebræ, so that the posterior concavity of the former and the anterior concavity of the latter are incompletely developed in the embryo and completely obliterated in the adult; and, further, that the second and third vertebral centra become indistinguishably fused, with the final result that in the adult the three centra are anchylosed into one apparently simple centrum. Hence it follows that in *Amiurus* the first intervertebral enlargement of the notochord is between the basioccipital and the body of the first vertebra, the second between the latter and the second vertebral centrum, and the third enlargement between the centra of the fourth and fifth vertebræ. The same observer has also pointed out that the neural canal over this composite centrum is bounded by a continuous tube of membrane bone, which originates near, and apparently replaces in the adult, the rudimentary cartilaginous neural arches of the third and fourth vertebræ in the embryo. The neural spines of the two vertebræ, on the contrary, are free at their distal extremities, although proximally they are continuous with each other and with the tube of the membrane bone.

For convenience in descriptive anatomy we venture to propose for the confluent second, third, and fourth vertebræ the term "complex vertebra." The extent to which the second vertebral centrum enters into the composition of the complex centrum is not altogether clear. According to RAMSAY WRIGHT (42), it "serves apparently merely to deepen the anterior concavity of the third vertebra, although in horizontal sections through Fish of 3 to 4 cm. in length the second and third vertebræ appear of almost equal size." But, from the description and figures, it would seem that the second and third centra together form the anterior third of the complex centrum, the remaining two-thirds representing the body of the fourth vertebra. On similar grounds we may perhaps regard the anterior third of the continuous neural arch of the complex vertebra, which is perforated for the exit of the dorsal and ventral roots of the fourth pair of spinal nerves, as belonging to the third vertebra, and the posterior two-thirds, similarly perforated for the transmission of the fifth pair of nerves, as representing the neural arch of the fourth vertebra.

Returning to *Macrones nemurus*, we find that that the centrum of the complex vertebra is much larger than any of the normal centra, and has its posterior concavity much deeper than the anterior (figs. 2, 4, and 5, *c.c.*). On the ventral surface of the centrum, near its anterior extremity, there is a pair of nutrient foramina (figs. 2 and 5, *n.f.*). In some Siluridæ, but not in *Macrones*, there is a second pair behind the first, and in that case it is evident that the two pairs are the normal nutrient foramina for the third and fourth vertebræ. The anterior extremity of the complex centrum is provided on its ventral surface with a pair of stout accessory articular processes, which incline forwards towards the corresponding processes of the basioccipital, but remain separated from them by the more slender articular processes of the centrum of the first vertebra (fig. 5). The centrum of the fifth vertebra is of still greater length, being about equal in this respect to the complex and first centra taken together (fig. 2, *c.*^{5}). Its anterior and posterior concavities are approximately equal in size, although the latter may sometimes be slightly the deeper of the two. Both the complex and fifth centra are not only greatly elongated but also laterally compressed, so as to present the appearance of a median bony keel when viewed from the ventral surface. The sixth centrum is much smaller, but nevertheless somewhat larger than the normal or but little modified centra that succeed it (figs. 1 to 3, *v.*^{6}). The body of the seventh vertebra (*v.*^{7}) resembles the normal free vertebral centra, except that its ventro-lateral margins are over-lapped by the splint-like posterior prolongations of the superficial ossifications. The remaining vertebral centra are normal and free.

The neural arches of the third and fourth vertebræ form the continuous bony walls of the neural canal in the region of the complex centrum; posteriorly they appear to be completely anchylosed with the arch of the fifth vertebra, which in turn is partially confluent with the arch of the sixth vertebra, at all events only very faint indications of sutures can be detected between them (fig. 2). In young specimens the arches of the fifth and sixth vertebræ are readily separable from each other, and also as a rule from the arch of the complex vertebra, the completeness of the coalescence being largely dependent on the age of the particular specimen examined. The arch of the seventh vertebra is usually quite distinct from its fellows with which, like the normal free vertebræ, it articulates by means of pre- and post-zygapophyses, but in old specimens it also may become partially anchylosed to the arch in front.

In a vertical longitudinal section of this part of the vertebral column, the bony walls of the neural canal are seen to be perforated on each side by successive pairs of small foramina for the exit of the dorsal and ventral roots of the fourth to the eighth pairs of spinal nerves inclusive (figs. 2, 5, see also p. 98).

The second vertebra has no distinct neural spine. The spine of the third vertebra forms a thin vertical and much elongated lamina of bone, which, like its neural arch, is inclined forwards in front, and articulates with the exoccipitals and supraoccipital, and is also overlapped along the greater part of its free dorsal edge by a spine-like backwardly-projecting process, derived from the supraoccipital (figs. 1, 2, 4, and 5, *n.s.*^{3}). The anterior margin of the lamina is much thickened, and, moreover, is slightly bifid, so as to clip, as it were, the posterior edge of the supraoccipital, at the junction of the latter with the two exoccipitals, but usually a small remnant of intercalated cartilage (fig. 5, *it.c.*) still persists between the two. The spine of the fourth vertebra is represented by a thickened spur of bone, of greater length than the foregoing, with which it is continuous anteriorly, and inclined obliquely backwards to such an extent as to overlap the much shorter and nearly vertical spines of the fifth and sixth vertebræ (fig. 2, *n.s.*^{4}). Its distal extremity is free and deeply cleft, so as to clip, and thereby support, the central portions of the two anterior interspinous bones of the dorsal fin. The spinous processes of the fifth, sixth, and seventh vertebræ are much shorter, and so crowded together as to be with difficulty distinguishable as separate elements, although sutures exist between them as well as between the spines of the fifth and fourth vertebræ. Their distal extremities are bifid, and support the proximal extremities of the first four interspinous bones (fig. 2). The succeeding spines are distinct and free from root to apex; they also are cleft to receive the remaining interspinous bones of the dorsal fin.

Between the forwardly inclined neural arch and spinous process of the third vertebra, behind and above, the body of the first vertebra below, and the posterior margin of the neural plate of the exoccipital in front, there is left on each side a somewhat triangular space where the lateral wall of the neural canal is formed only by a tough, fibrous membrane, in which the claustrum and the ascending processes of the "incus" and "stapes" are imbedded (figs. 1, 2, 4, and 5).

Neither the first nor the second vertebra has any trace of transverse processes, and in the third vertebra these structures may be represented by the two "mallei." The transverse processes of the fourth vertebra on the other hand are enormously developed, forming on each side of the complex vertebra an expanded wing-like lamina of bone, the flat root of which has its origin not from the centrum, but from the whole length of the continuous neural arches of the third and fourth vertebræ (figs. 1, 3, and 4, *t.p.*^{4}). The under surface of each outgrowth is comparatively smooth, and slightly concave from before backwards, but its dorsal surface is traversed by one or two stout ridges radiating outwards from the neural arch. An oval cleft, near the anterior extremity of its distal margin, partially subdivides each lamina into an anterior and a posterior division, of which the former is somewhat the longer of the two (*t.p.*^{4}*a.*, *t.p.*^{4}*p.*). The anterior division (*t.p.*^{4}*a.*) has a thick root, continuous behind with the thinner and more lamellar posterior division, which bends slightly downwards towards its distal end, and is ultimately prolonged into a slender free process that curves sharply downwards and then outwards and a little backwards, the concavity of the curvature being directed outwards (fig. 3, *tp.*^{4}*a.*). At the extremity of the thickened proximal portion of the division, where the latter joins its crescentic distal prolongation, there is an oval facet which looks forwards and outwards, and articulates with a similar articular facet on the inferior limb of the post-temporal bone, near the ventral margin of the post-temporal plate (figs. 1 and 4, *pt.f.*). The posterior division (*tp.*^{4}*p.*) is broad and comparatively thin, except that its dorsal surface is strengthened by a stout oblique ridge extending outwards from the neural arch towards the distal margin of the process. Its posterior edge overlaps and is partially anchylosed to the proximal half of the succeeding transverse process, leaving however the distal portion as a broad, free process of bone (figs. 1 and 3). Unlike the anterior division, the posterior is horizontally disposed and bears a greater resemblance to a normal transverse process in being directed slightly upwards as well as outwards. Except for its greater length, and the width of its root, which, like that of its predecessor, springs from the arch of its vertebra, the transverse process of the fifth vertebra more nearly resembles an ordinary rib-bearing process. The distal end is free, being separated by an oval cleft from the process in front, but proximally the two are confluent (figs. 1 and 3, *tp.*^{5}).

It will be obvious that the modified transverse processes of the fourth and fifth vertebræ combine to form on each side of the complex and fifth vertebræ an almost continuous bony plate, with a smooth and slightly concave ventral surface and a strongly deflected anterior margin, which is adapted and intimately applied to the convex dorsal and anterior walls of the anterior third of the air-bladder.

The transverse processes of the sixth vertebra are normal except for the slight coalescence of their roots with the corresponding processes of the fifth vertebra. Their origin is from the centrum and not from the neural arch, and their distal extremities carry the first pair of ribs (figs. 1 and 3, *tp.*^{6}, *r.*′).

Each of the lateral surfaces of the complex centrum is traversed close to its anterior margin by a faint ridge (fig. 4, *l.r.*), which, commencing at the base of the accessory articular processes, passes obliquely backwards and upwards, and apparently indicates the anterior limit of the superficial bony deposit which invests both sides of the centrum. To the dorsal portion of this ridge, which may be called the "lateral ridge" of the complex centrum, there is firmly attached, but except in old specimens not actually confluent with it, an elongated nodule of bone which terminates at its dorsal extremity in a thickened nodular prominence (figs. 3 and 4, *r.n.*). From the relations of this ossicle to the radial fibres of the malleus we shall in future refer to it as the "radial nodule." The radial nodule generally coincides with the junction of the anterior third of the complex centrum with the posterior two-thirds, and according to RAMSAY WRIGHT, by whom, in *Amiurus*, it is apparently referred to as the "oblique ridge," indicates the line of union of the third and fourth vertebral centra in the formation of the complex centrum. In young specimens the nodule is united by fibrous tissue only to the lateral ridge but in older forms appears to become firmly anchylosed thereto. From the thickened dorsal extremity of the radial nodule, but separated therefrom in young specimens by a well-marked suture, a thin, narrow strip of bone (fig. 3, *d.l.*) extends obliquely backwards and outwards ventrad to the cardinal groove, which, in consequence, becomes at this point a complete canal, and ultimately passes on to the ventral surface of the posterior division of the transverse process of the fourth vertebra, and blends therewith by its anterior margin and pointed distal extremity, leaving, however, its posterior edge projecting in the form of a faint ridge. In mature or old specimens this process, which we shall call the "dorsal lamina," and the lateral ridge, form a continuous obliquely-disposed ridge of bone stretching from the side of the complex centrum to the transverse process of the fourth vertebra, the radial nodule then appearing as a small nodular projection from its surface.

A thin but continuous superficial ossification more or less completely invests each side of the complex and fifth centra, and obscures all external indication of the intervertebral suture which separates them (figs. 1 and 3, *s.os.*). Each ossification is somewhat triangular in shape, with the broad base coincident with the ventro-lateral margins of the two centra, and its anterior and posterior margins converging towards the flattened root of the transverse process of the fourth vertebra, where the apex terminates beneath the cardinal groove (*cd.g.*) by becoming suturally united with the oblique posterior or inner margin of the dorsal lamina (fig. 3). The anterior margin of each ossification coincides with, and indeed, appears to form, the oblique lateral ridge of the complex centrum. Traced posteriorly, each superficial ossification gradually contracts and partially exposes the lateral surface of the fifth vertebral centrum, but is, nevertheless, continued as a narrow splint of bone along the ventro-lateral edge of the succeeding centra as far as the seventh (fig. 3). The free ventral margins of the two ossifications and their splint-like prolongations project downwards beyond the ventral surfaces of the different vertebral centra with which they are in relation, so as to form the lateral boundaries of a deep but narrow median groove extending from the first to the seventh vertebra (figs. 3 and 23, *a.g.*). The lateral margins of the anterior extremity of the groove are formed by the paired accessory articular processes of the basioccipital and the centra of the first and complex vertebræ. The groove has a fibrous ventral wall, in part, at least, formed by the median portion of the dorsal wall of the anterior chamber of the air-bladder, and in the canal, so constituted the anterior section of the dorsal aorta is lodged. In the dry skeleton paired nutrient foramina may be seen in the dorsal wall of the groove, leading into the different vertebral centra; of these foramina one pair only belongs to the complex centrum (fig. 3). Between the dorsal edge of each superficial ossification and the root of the transverse process of the fourth vertebra, the lateral surface of the complex centrum is traversed by a deep groove which, anteriorly, is converted for a short distance into a complete canal by the extension of the dorsal lamina from the radial nodule to the ventral surface of the transverse process (fig. 3, *cd.g.*). Through this groove and short canal, the posterior cardinal vein passes forwards to its junction with the anterior cardinal in front, the union of the two veins to form the Cuvierian duct taking place in a somewhat triangular fossa situated immediately anterior to the radial nodule. The attenuated anterior lobes of the mesonephros accompany the posterior cardinal veins as they extend forwards to their terminal lymphoid enlargements in front of the air bladder. In correspondence with the asymmetrical development of these veins the left cardinal groove is much narrower than the right.

It will be noticed (fig. 3) that the dorsal edge of the posterior half of each superficial ossification forms the ventral lip of the cardinal groove of its side, and also, in conjunction with the hinder margin of the dorsal lamina, gives rise to a Λ-shaped ridge, the two arms of which converge from the ventro-lateral margins and sides of the fifth and sixth vertebral centra, and from the ventral surface of the transverse process of the fourth vertebra, eventually uniting on the root of the latter, near the junction of the body of the fifth vertebra with the complex centrum. These converging ridges coincide with the line of attachment of the dorsal margins of the primary transverse septum of the air-bladder to the skeleton.

It is mainly owing to the growth of the investing superficial ossification and their downward projection beyond the ventral margins of the anterior vertebral centra that the vertebral column presents the appearance of a thin, laterally compressed, median bony keel, when viewed from the ventral surface.

The Cranium.—In common with all Siluroid Fishes the skull in *Macrones* exhibits not a few features wherein it differs considerably from the normal Teleostean type, but we shall here refer in detail only to such of its structural peculiarities as are more or less closely correlated with certain characteristic modifications of the membranous labyrinth of the internal ear.

The dorsal surface of the hinder part of the skull (figs. 1 and 4) is formed by the supraoccipital (*s.o.*), the epiotic (*ep.o.*), the pterotic (*pt.o.*), and the sphenotic (*sp.o.*) bones. In the absence of distinct parietal bones the supraoccipital is exceptionally large; anteriorly it is deeply cleft by the posterior cranial fontanelle, while posteriorly it is produced into a spine-like process which extends backwards dorsad to the confluent spines of the third and fourth vertebræ as far as the first interspinous bone of the dorsal fin (fig. 1, *so.′*). Laterally, the supraoccipital articulates with the epiotics, pterotics, and sphenotics; anteriorly with the frontals, and below with the exoccipitals. The posterior face of the bone, immediately over the foramen magnum, is traversed by a median ridge which, superiorly, is confluent with the horizontally flattened root of the supraoccipital spine (fig. 6), and on each side of the ridge, just beneath the root of the spine, there is a small foramen for the transmission of the lateral branch of the fifth cranial nerve (fig. 6, V^l.).

Each exoccipital (figs. 1 to 7, *eo.*) consists of a thin, laterally compressed neural plate, which is situated at the side of the foramen magnum, and meets the supraoccipital above, and, in addition, is prolonged forwards into the cranial cavity as a vertical plate of bone, the free anterior edge of which forms the posterior boundary of a large aperture leading from the general cranial cavity into a spacious lateral recess in which the utriculus and its semicircular canals are lodged (figs. 2 and 5, *eo.′*). From the outer surface of its neural plate each exoccipital gives off a posterior plate which extends outwards at right angles to the foregoing on to the hinder face of the skull and there articulates dorsally with the supraoccipital and the epiotic (fig. 6, *eo.*^{2}). The posterior plate eventually extends round the postero-lateral angle of the cranium on to the lateral surface, where it occupies the place normally taken by the opisthotic in most other Teleostean Fishes, meeting the prootic in front, the lateral margin of the basioccipital below and the pterotic and epiotic bones above (figs. 3 to 5, *eo.*^{3}). The opisthotic plate of the exoccipital is extremely thin, and, in the complete absence of a true opisthotic element, is in relation internally with the inferior part of the arch of the posterior vertical semicircular canal. A small foramen perforates the anterior margin of the plate, near its junction with the prootic, and transmits the glossopharyngeal nerve (fig. 4, IX.), and somewhat more posteriorly there is a much larger aperture for the exit of the vagus (X.). The hypoglossal or first spinal nerve emerges from the cranial cavity through a small foramen in the posterior plate, situated in the lower part of the angle which the latter makes with the neural plate (fig. 4, *sp.n.′*).

The basioccipital (figs. 1 to 8, *b.o.*) has a concave posterior face provided on its ventral margin with a pair of stout accessory articular processes for articulation with a pair of precisely similar processes on the adjacent ventral edge of the centrum of the first vertebra (figs. 4 to 6). Anteriorly to these and on each of its lateral surfaces the basioccipital is furnished with a pair of short but stout processes for articulation with the doubly-facetted inner extremity of the inferior limb of the post-temporal (figs. 1, 4, and 6). Midway between the two series of articular processes the ventral surface of the basioccipital is perforated by a single median nutrient foramen (fig. 3). Dorsally the bone suturally articulates with the inferior margins of all three ex-occipital plates.

The superior or cranial surface of the basioccipital is deeply excavated to form the floor, and to some extent the side walls also, of three fossæ, one median, the "cavum sinus imparis" of WEBER, and two lateral, the "foveæ sacculi." Horizontal ingrowths from the inner surfaces of the exoccipitals meet over the dorsal surface of the basioccipital and either fuze or remain separated by a median suture, thereby forming a thin bony roof for the three fossæ, and, at the same time, a section of the cranial floor on which the medulla oblongata rests (figs. 6 to 8, *e.o.*^{4}). The floor and side walls of the cavum sinus imparis are furnished by the basioccipital alone, and its roof by the horizontal exoccipital plates; the floor and inner walls of the foveæ sacculi are also supplied by the basioccipital, their thin roof by the exoccipitals, but the thin outer walls are mainly formed by the inferior margins of the opisthotic plates of the exoccipitals (figs. 5, 7 to 9, *c.s.i.*, *f.s.*). A comparison of these figures will sufficiently illustrate the mode of formation and mutual relations of the three fossæ. In fig. 8 the roof of the skull has been removed in order to show the floor of the cranial cavity and the horizontal plates of the exoccipitals *in situ* (*e.o.*^{4}). In fig. 9 these plates have been partially removed so as to expose the cavum (*c.s.i.*) and foveæ (*f.s.*), and their respective contents the sinus endolymphaticus (*s.e.*) and the two sacculi (*s.*). Fig. 5 represents a vertical longitudinal section through the cranium, bisecting the cavum sinus imparis (*c.s.i.*); while fig. 7 was drawn from a transverse section through the hinder part of the skull of *Macrones aor*, and shows the cranial cavity separated from each utricular recess by the intracranial prolongation of the neural plate of the exoccipital (*e.o.*$'$), and also the relative positions of the cavum and the two foveæ (*c.s.i.*, *f.s.*). From fig. 7 it will be apparent that the cavum and the foveæ lie parallel to one another, but inasmuch as the latter are situated more towards the sides of the basioccipital they occupy a slightly lower level, and individually are, perhaps, somewhat smaller than the former.

The foveæ sacculi end blindly behind but in the dry skeleton the cavum sinus imparis communicates by means of a triangular and slightly constricted aperture with the neural canal over the hinder edge of the basioccipital (figs. 5, 6, and 8, *c.s.i.*). This aperture may be readily seen in a view of the posterior face of the skull, beneath the hinder margin of the roof of the cavum (figs. 6 and 8, *c.s.i.*). In the fresh specimen, on the contrary, the aperture places the cavum in communication with two small laterally-situated cavities which lie on the dorsal surface of the hinder part of the basioccipital, behind the posterior edge of the bony roof of the cavum, and have partly osseous and partly thick fibrous walls—the "atria sinus imparis" of Weber. In figs. 4, 5, and 8, it will be noticed that the posterior edge of each exoccipital, beneath the origin of its horizontal plates that roof in the cavum sinus imparis and foveæ sacculi, is deeply notched by a semicircular emargination; this notch forms the anterior half of the external atrial aperture, or "apertura externa atrii" of Weber, which normally is completely closed by the spoon-shaped process of the stapes of its side. Anteriorly the cavum and foveæ open into a deep transverse groove in the cranial surface of the basioccipital, situated just in front of the anterior margin of their bony roof (figs. 5 and 8, *t.g.*). The opening of the cavum is by means of a relatively small and somewhat triangular median aperture; the foveæ by two laterally situated, relatively large, and somewhat rounded orifices (fig. 5, *f.s.*) On each side the transverse groove communicates by a deep, but narrow, slit-like prolongation with the lateral recess of the cranial cavity (*ut.r.*) in which the utriculus and its semicircular canals are lodged (figs. 5 and 8, *l.g.*). The transversely disposed groove contains the ductus endolymphaticus, and its slit-like lateral prolongations, the ductus sacculo-utricularis of that side (fig. 9, *d.e.*, *d.s.u.*). At the bottom of the transverse groove the dorsal surface of the basioccipital is raised into a sharp median ridge (fig. 8) which divides behind as it passes beneath the horizontal roofing plates of the exoccipitals into two divergent vertical ridges, and these by their union above with the exoccipital plates form the outer walls of the cavum sinus imparis and at the same time the inner walls of the two foveæ sacculi (fig. 7). Anteriorly also the ridge divides, but into two horizontally diverging arms which together form the anterior rim of the transverse groove (fig. 8). In front of the transverse groove the two prootics meet in a median suture in the floor of the cranial cavity. In close proximity to this suture the posterior margin of each prootic is produced into a slender, backward-projecting spur of bone which forms the anterior lip of the groove for the ductus sacculo-utricularis and also overlies the entrance to an excavation in the substance of the prootic into which the contracted anterior extremity of the sacculus penetrates.

As is the case in all Teleostei the inner wall of each auditory capsule is deficient and hence the latter appears as a deep lateral recess of the hinder part of the cranial cavity (figs. 5 and 8, *ut.r*). Externally each recess is bounded by the prootic, sphenotic, pterotic, and epiotic bones, and also by the posterior opisthotic plates of the exoccipital; internally, each recess is in wide communication with the general cranial cavity. The entrance to each recess from the cranial cavity is bounded by two prominent ridges, one in front and the other behind, which slightly constrict the communication between the two cavities (fig. 5). The anterior ridge is developed from the inner surface of the prootic, and its free edge is directed obliquely backwards, while the posterior ridge, which is really the intracranial prolongation of the neural plate of the exoccipital, looks directly forwards. Each recess is prolonged backwards to the outer side of this portion of the exoccipital until it becomes closed behind by the posterior plate of the same bone and by the epiotic. (See transverse section of this part of the skull in fig. 7.)

In places the outer walls of the auditory capsules are extremely thin, and this is notably the case where they are formed by the epiotic and prootic bones and by the opisthotic plates of the exoccipitals. Over definitely circumscribed areas these bones are almost transparent when the skull is held up to the light.

Although foreign to the subject of this paper, it may be mentioned that at each postero-lateral angle of the skull there is a deep fossa, closed internally but open externally, and formed by the opposition of correlated grooves in the pterotic and epiotic in front and behind respectively, and by the supraoccipital internally and superiorly (figs. 1, 4, and 6, *tp.f.*). RAMSAY WRIGHT (43), in his description of the skull of *Amiurus catus*, throws out the suggestion that these fossæ may be the atrophied rudiments of somewhat similar cavities described by SAGEMEHL* as present in *Amia calva*, and by him termed the temporal fossæ. In *Macrones* each fossa fulfils the function of an articular cavity for the proximal extremity of the ascending process of the post-temporal (fig. 6).

The Pectoral Girdle.—The post-temporal (supra-clavicle of RAMSAY WRIGHT and others) is the only element of the shoulder-girdle that, for our purpose, requires any special description.

As in most other Teleostei, the post-temporal is somewhat V-shaped, its two divergent arms articulating with the postero-lateral angle of the skull and its stem with the proximal extremity of the clavicle (figs. 3 and 6). Of the two arms, one, the ascending process, is somewhat loosely inserted into the temporal fossa of its side (fig. 6, *pt.a.*), while the other, or inferior limb (*pt.i.*), articulates by a doubly-facetted step-like inner extremity with a pair of suitably modified processes on the lateral surface of the basioccipital. Externally the two processes converge, and eventually unite to form the post-temporal stem (fig. 6, *pt.s.*). The latter is a flattened process of bone continuous superiorly with the ascending process, and so superficially situated that its outline is readily seen on the external surface of the body behind the posterior edge of the operculum (fig. 15, *pt.*). From the inner surface of the stem, and also from the adjacent ventral margin of the inferior limb, a relatively thin, transversely-disposed plate of bone grows downwards, and is so arranged that its two surfaces look directly forwards and backwards respectively (figs. 3 and 6, *pt.p.*). The posterior face of each plate is comparatively smooth, and at the same time faintly concave, and, moreover, is so applied to the crescentic extremity of the anterior division of the transverse process of the fourth vertebra as to fill up the concavity of the latter, and also project outwards beyond it (fig. 3). In fact, the outer portion of the post-temporal plate completes the circumference of a circular bony structure, of which the ventral and inner margins are furnished by the crescentic process. The latter also helps to slightly deepen the concavity of the posterior face of the plate by strengthening as it were its inner and ventral lips. Along the dorsal and inner margins of the posterior face of each plate there is a curved facet for articulation with a similarly shaped surface on the adjacent anterior edge of the root of the crescentic process (fig. 6, *f.*). The anterior face of the plate, which is greatly thickened towards the centre, is somewhat convex, and is also traversed by a groove continued dorsally into a deep tubular socket for the reception of the slender proximal extremity of the clavicle (fig. 6, *cl.s.*). Both the post-temporal plate and the stem of the bone are on each side firmly united to the crescentic extremity of the transverse process by ligamentous fibres, which, in turn, blend with the lateral margins of the transverse and aponeurotic membranes (*vide* p. 88). The union of each plate with the crescentic process is further strengthened by a strong ligament which passes between the concave margin of the latter and a slight depression near the inner edge of the posterior face of the former (fig. 3, *lgt.*). The post-temporal plates and the two crescentic processes combined form two slightly concave bony structures which are closely applied to the corresponding lateral portions of the anterior wall of the air-bladder (fig. 3).

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* "Beiträge zur vergl. Anat. der Fische. Das Cranium von *Amia calva*." 'Morphol. Jahrbuch,' vol. 9, 1883.

The clavicle (fig. 3, *cl.*), in addition to a slender head articulating with the post-temporal in the manner described, has a well-marked posterior process projecting backwards dorsad to the articulation of the pectoral fin, but considerably ventrad to the distal extremities of the modified transverse processes of the fourth and fifth vertebræ (*cl.p.*).

The lateral line canal traverses a well-marked groove in the outer surface of the ascending process of the post-temporal as it passes forwards from the lateral surface of the trunk to the skull.

The Auditory Organ.—We are not acquainted with any recorded observations as to the structure and relations of the various parts of the membranous labyrinth in *Macrones*, and the results of our own dissections are such that we have but little to add that is not merely confirmatory of the investigations of previous observers in other Siluroids, but as so very few species have been examined a brief description of the internal ear of *Macrones* may not be altogether superfluous.

A comparison of figs. 8 and 9 will serve to indicate the relations of the different factors of the membranous labyrinth to one another and to the osseous chambers in which they severally lie. In fig. 9, the fibrous roof of the atria sinus imparis has been removed, and also the bony roof of the cavum sinus imparis and foveæ sacculi, so as to show the mutual relations of the two sacculi, the sinus endolymphaticus, and the ductus endolymphaticus to one another and to the rest of the internal ear, as well as the relations of the sinus endolymphaticus to its cavum and to the two atria into which the latter opens posteriorly.

The utriculus (fig. 9, *ut.*) is a somewhat oblong sac lying in, but without completely filling, the utricular recess (figs. 7 and 8, *ut.r.*), and sharply constricted off from the sacculus (fig. 9, *s.*) although connected with the latter by a short but comparatively narrow ductus sacculo-utricularis (*d.s.u.*). The three semicircular canals connected with each utriculus traverse the various periotic bones with which they are in relation for only a very limited portion of their extent, and for the most part lie free in the utricular recess. The arch of the posterior vertical canal (*p.v.c.*) traverses the supraoccipital and epiotic; the horizontal canal (*h.c.*) occupies a groove on the inner surface of the epiotic, and for the remainder of its course a short canal in the pterotic; the anterior vertical canal (*a.v.c.*) has its arch but slightly protected by a short canal in the prootic and a deep groove in the sphenotic. An oblique valve, similar to that described by Ramsay Wright (43) in the case of *Amiurus catus*, is also to be found in the narrow lumen of the ductus sacculo-utricularis of *Macrones*.

The sacculus (fig. 9, *s.*) is an elongated sac, expanded and somewhat pear-shaped behind, but tapering in front. Its narrow anterior extremity penetrates into a slight excavation in the hinder margin of the prootic, but the posterior portion, with its lagæna cochleæ, occupy a bony chamber of a similar shape—the fovea sacculi—the formation of which has already been described. From the inner surface of the sacculus, before the latter enters its fovea, a thin-walled transverse duct is given off, which extends inwards, and in the median line of the floor of the cranial cavity joins the corresponding duct of the opposite side, and the two together constitute the transversely disposed ductus endolymphaticus (*d.e.*). The ductus occupies the deep transverse groove in the cranial surface of the basioccipital (figs. 5 and 8, *t.g.*), while the ductus sacculo-utricularis traverses a slit-like groove leading from the transverse groove into each utricular recess (*l.g.*). At a point where the two canals unite the ductus endolymphaticus gives off a median, pear-shaped, and extremely thin-walled sinus endolymphaticus (the "sinus impar" of Weber) which projects backwards into, and almost fills, the cavum sinus imparis (fig. 9, *s.e.*).

In our description of the mode in which the cavum sinus imparis and the foveæ sacculi are formed we stated that the latter were closed behind, but that the former in the dry skeleton, communicated freely with the neural canal over the dorsal surface of the hinder part of the basioccipital. In the fresh specimen, on the contrary, the cavum widens out round the blind posterior extremities of the two foveæ into two small, laterally-situated, and nearly spherical cavities (the "atria sinus imparis" of Weber) which lie on the upper surface of the posterior part of the basioccipital, and have partly bony and partly fibrous walls (fig. 9, *at.*). The roof of the atria is formed anteriorly by an extension backwards of the bony roof of the cavum sinus imparis, and posteriorly by a prolongation forwards of the fibrous posterior wall. The posterior wall of the two atria is formed by a thick mass of fibrous tissue (*p.w.*) which rests on the dorsal surface of the centrum of the first vertebra, between the pit-like sockets for the reception of the two condylar processes of the stapedes, and dorsally is continued forwards as a roof to the atria, as far as the hinder edge of the roof the cavum sinus imparis, where it apparently becomes continuous with the very thin layer of dura mater investing the inner surface of the cranial bones. In the anterior wall is the median foramen, through which the two atrial cavities freely communicate with the cavum sinus imparis, but on each side of this the anterior wall is formed by the concave posterior edge of the root of the exoccipital. The floor of the atria is formed by the basioccipital, while their outer walls coincide with two deep semicircular notches in the posterior margins of the exoccipitals. The notch in each exoccipital, with the adjacent dorso-lateral margin of the basioccipital, form the anterior, superior, and inferior boundaries of a lateral orifice (*at.a.*), the "apertura externa atrii" of WEBER—by which each atrium would communicate with the exterior of the skull were it not that the aperture is completely closed by the spoon-shaped extremity of the "stapes" of its side (fig. 9, *sc.s.*, also figs. 4 and 5, *at.a.*). The posterior boundary of each external atrial aperture is formed by the same thick mass of fibrous tissue that forms the posterior atrial wall. The inwardly curved inferior extremities of the two claustra lie immediately over the external atrial apertures, and may help to strengthen their dorsal lips, and possibly also contribute to the support of the atrial roof. The two atrial cavities are in open communication with each other and with the cavum sinus imparis anteriorly; in fact, if it were not for a thick vertical ridge of fibrous tissue projecting inwards from the median line of their posterior wall (fig. 9), they might be regarded as constituting a single transversely-disposed chamber. Essentially, the two atria may be considered as forming a bilobed posterior prolongation of the cavum sinus imparis excavated in the substance of a thick mass of fibrous tissue which forms the floor of the neural canal over the body of the first vertebra and the contiguous dorsal surface of the basioccipital. The fibrous tissue forming the roof and posterior wall of the atrial cavities is continuous laterally with the fibrous walls of the neural canal between the arch of the third vertebra behind, and the exoccipitals in front.

In his account of these structures in *Amiurus*, RAMSAY WRIGHT (43) describes an anteriorly bilobed median excavation in the substance of the tissue overlying the medulla oblongata which is said to communicate on each side with the atrial cavities. This excavation or receptaculum dorsale is described as being "filled with the same fluid contents as the atria and cavum." A precisely similar receptaculum exists in *Macrones*, and communicates with the atrial cavities by an aperture, which, on each side, perforates their fibrous roof near the superior border of the spatulate portion of the "stapes."

From the position and relations of the various factors of the membranous labyrinth and of the bony chambers or recesses in which they lie, it will follow that the perilymph will not only surround the utriculus and semicircular canals, but also extend into the foveæ sacculi and cavum sinus imparis, and surround their respective contents, the sacculi and sinus endolymphaticus, eventually filling the two atrial cavities and bathing the inner surfaces of the spoon-shaped processes of the "stapedes."

The Weberian Ossicles.—A series of moveably interconnected ossicles which, morphologically, are modified portions of the three anterior vertebræ, serve to connect the membranous labyrinth with the air-bladder and thereby establish close physiological relations between the two structures. As we have already pointed out, the most anterior of these in *Macrones* fits into and completely closes the external atrial aperture of its side and is therefore in contact by its inner surface with the perilymph; the most posterior of its ossicles has the hinder half imbedded in the dorsal wall of the anterior chamber of the air-bladder. Fig. 24 shows the general relations of the ossicles to one another, and to the membranous labyrinth and air-bladder, and in figs. 3 to 5 they are represented as they appear *in situ.*[*]

In *Macrones* each claustrum (figs. 4, 5 and 10, *c.*) is imbedded in the fibrous wall of the neural canal between the arch of the third vertebra and the exoccipital, and lies at the side of the foramen magnum, immediately behind, and almost in contact with, the posterior edge of the neural plate of the exoccipital. It is a slender spicular bone, slightly curved at its lower extremity where it is received into the angle between the ascending and spatulate processes of the scaphium, and separated by the somewhat contracted root of the latter process from the body of the first vertebra (figs. 4 and 5, *c.*). The upper extremity of the ossicle is in contact with, and may even extend into, the intercalated cartilage between the spine of the third vertebra and the supraoccipital, while the inferior incurved extremity coincides with the level of the posterior margin of the roof of the cavum sinus imparis and extends into and helps to strengthen the roof of the atrial cavity of its side. Although in close contiguity with the scaphium by its lower extremity, the claustrum is not specially attached to it, nor does it appear that the claustrum can in any way control or influence the movements of the scaphium.

The scaphium (figs. 10 and 11, also figs. 4 and 5, *sc.*) lies just behind the claustrum, and consists of two processes united at a right angle, an ascending process (figs. 10 and 11, *sc.a.*) and a horizontal or spatulate process (*sc.s.*). The former is imbedded in the fibrous wall of the neural canal behind and parallel to the claustrum (figs. 4 and 5, *sc.a.*), and consists of a slender spicule of bone with a slight forward curvature and a pointed upper extremity; the latter, which has its origin from the inferior extremity of the ascending process by a somewhat contracted root, passes horizontally forwards over the dorso-lateral edge of the centrum of the first vertebra and beneath the lower extremity of the claustrum, and finally terminates on the lateral margin of the dorsal surface of the basioccipital in a characteristic spoon-shaped expansion, which is concave on its inner surface and convex externally (figs. 4 and 5, *sc.s.*). The spatulate process is so adapted, as regards shape and size, as to accurately fit into and completely occupy the semicircular notch in the posterior margin of the exoccipital, and consequently to form by its inner concave surface the outer wall of the atrial cavity of its side, and completely close the corresponding external atrial aperture (figs. 4, 5, and 9, *sc.s.*). The margin of the concavo-convex portion of the spatulate process is attached by fibrous tissue to the lips of the atrial aperture, but the connection is nevertheless sufficiently loose to admit of the process undergoing a slight inward or outward movement, according to the direction in which the scaphium rotates on its condylar process, and any such movement will necessarily lead to a slight diminution or increase in the size of the atrial cavity. Enlargement of the atrial cavities will take the form of lateral extension round the concave posterior edge of the root of the exoccipital (*vide* fig. 8, *at.a.*). On the inferior side of the junction of the spatulate and ascending processes there is a small spherical cartilage-tipped condyle, which fits into a cup-shaped socket provided for it on the dorso-lateral surface of the centrum of the first vertebra (figs. 10 and 11, *sc.c.*; also fig. 5, *sc.*). The inner extremity of a stout tendinous interossicular ligament is attached to the outer surface of the spatulate process, and serves to connect the scaphium with the anterior extremity of the tripus (fig. 12, *i.lg.*, also figs. 9 and 4).

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[*] For reasons already given (5), we have suggested that the names applied to three of these ossicles, by WEBER, viz., "malleus," "incus," and "stapes," may, with advantage, be replaced by "tripus," "intercalarium," and "scaphium," respectively, retaining, however, the term "claustrum" for the fourth ossicle, while for the ossicles collectively, we suggested the name "Weberian" in preference to "auditory."

Like the scaphium the intercalarium consists of ascending and horizontal processes united at nearly a right angle (figs. 9 to 12, *in.*, also figs. 4 and 5). Both processes are extremely slender and brittle. The ascending process (fig. 10, *in.a.*) lies in the fibrous wall of the neural canal behind and parallel to the corresponding process of the scaphium and immediately in front of the arch of the third vertebra (figs. 4 and 5, *in.*). At its lower extremity the process becomes continuous by a slightly open curvature with the horizontal portion of the ossicle (figs. 10 and 12, *in.h.*). The latter process is directed outwards and a little forwards, and eventually terminates in a discoidal expansion imbedded in the substance of the interossicular ligament exactly midway between the insertion of the latter into the spatulate process of the scaphium and its external attachment to the anterior end of the tripus (fig. 12, *in.h.*). The intercalarium differs from both the tripus and scaphium in having no connection or articulation with any vertebral centrum or other part of the skeleton; nevertheless, its ascending process is capable of a limited amount of rotation on its own axis as the horizontal process moves backwards or forwards with the lateral motion of the tripus and the consequent pull of the interossicular ligament.

The interossicular ligament (figs. 9, 12, 21, and 22, *i.lg.*; also fig. 4) is a short but relatively to its length, extremely thick, transversely-disposed ligament, composed of glistening tendinous fibres of a yellowish colour, and stretching between its attachment to the outer surface of the spatulate process of the scaphium internally and its insertion into the anterior extremity of the tripus externally. The insertion of the discoidal extremity of the horizontal process of the intercalarium into the middle of the ligament completely divides the latter into two portions, the fibres from the scaphium being inserted into the inner face of the disc, while those passing to the tripus have their origin from its external face.

The tripus (figs. 12 to 14, *tr.*) differs considerably in shape from both the scaphium and intercalarium, and is a much larger ossicle than either. In shape it is a thin flattened bone with its surfaces looking respectively upwards and downwards and its margins inwards and outwards. The whole extent of the outer margin is convex, but much more so posteriorly than anteriorly; its inner margin, on the other hand, presents two concavities, a very slight anterior one, but a much deeper one posteriorly. As the tripus passes forwards from its posterior insertion into the dorsal wall of the air-bladder to its ligamentous connection with the intercalarium and scaphium in front it lies along the lateral surfaces of the complex centrum and the body of the first vertebra, and for the hinder two-thirds of its extent is in close relation by its dorsal surface with the under side of the broad flat root of the transverse process of the fourth vertebra (figs. 3 and 4, *tr.a.*, *tr.c.*). The ossicle is divided into three well-marked and extremely characteristic processes which have much the same general relations to one another that the ramus, the condyle, and the angular process have in the Mammalian lower jaw. For reasons which will be sufficiently obvious we may designate them the anterior, articular, and crescentic processes. The anterior process (figs. 12 to 14, *tr.a.*) lies along, and parallel to, but by no means in contact with, the lateral surfaces of the body of the first vertebra and the anterior third of the complex centrum, or, more strictly speaking, in a line with the junction of the dorsal and lateral surfaces of those centra, but its anterior extremity projects so far in front of the centrum of the first vertebra as to be exactly opposite the external atrial aperture, and the convex outer surface of the spatulate process of the scaphium (figs. 4, 9, 21, and 22). The anterior process is a thin, flattened, lamina of bone, slightly convex along the outer margin, and as faintly concave on its inner border. The somewhat greater length of its outer as compared with the inner margin, gives to the truncated anterior extremity of the process a slightly thickened and nearly straight edge, which looks directly inwards towards the spatulate process of the scaphium, and it is to this thickened edge that the outer extremity of the interossicular ligament is attached. The crescentic process is a direct continuation backwards of the anterior process, and, like the latter, is thin and flattened, although much more slender. Normally, the whole of the process, with the exception, perhaps, of a small portion of its root, is imbedded in the tunica externa of the corresponding half of the dorsal wall of the anterior compartment of the air-bladder (figs. 18 and 19, *tr.c.*). The root of the crescentic process is in a line with the anterior process, but for the posterior two-thirds of its extent the process becomes more slender, and at the same time, rather abruptly bent inwards upon itself, so that its posterior, or, more correctly, its inner extremity, which is slightly decurved, is in contact with the lateral surface of the complex centrum at a point behind and above the thickened dorsal extremity of the radial nodule (fig. 3). In shape the process greatly resembles a sickle, having its inner concave edge partially encircling the radial nodule, and its convex outer margin directed at first outwards, and then bent directly inwards. From the convex outer margin, and at the point where the process first commences to curve inwards towards the complex centrum, a slender heel-like process is given off which is directed outwards and a little forwards towards the antero-lateral angle of the air-bladder (figs. 12 to 14, *tr.h.*; also figs. 3, 18, and 19). Although not in actual contact, the crescentic process, the root of the transverse process of the fourth vertebra, is intimately related to its dorsal surface. The articular process of the tripus is a somewhat triangular outgrowth from the inner margin of the ossicle at the junction of its anterior and crescentic processes (figs. 12 to 14, *tr.ar.*). The process is flattened in a horizontal plane, and its upper and lower surfaces coincide in direction with those of the remainder of the ossicle. Near the anterior margin of its dorsal surface there is a thin vertical ridge, which slopes upwards towards the distal or inner extremity of the process, and then becomes a vertical elongated condyle (fig. 13, *dr.*). The condyle articulates with the lateral surface of the anterior third of the complex centrum, that is, the centrum of the third vertebra, at the bottom of the deep pit-like depression, situated immediately in front of, and dorsad to, the radial nodule. A vertical ridge also traverses the ventral surface of the crescentic process, commencing at the root of the heel-like process, and from thence extending obliquely forwards and inwards on to the ventral surface of the articular process (figs. 12 and 14, *v.r.*) The ridge lies much nearer to the inner than the outer margin of the crescentic process, and for a part of its course follows the curvature of the former. Only a slight interval separates the anterior end of the ridge from the thickened dorsal portion of the radial nodule, the two being exactly opposite each other (figs. 3 and 20). We shall call this ridge the ventral ridge of the tripus.

The tripus is freely moveable in a lateral plane on its articulation with the complex centrum by means of the articular process, and it is evident that its anterior and crescentic processes represent the two arms of a lever, the fulcrum of which is the vertebral connection of the articular process.

We append the following measurements of the Weberian ossicles of a specimen of *Macrones nemurus* eight inches in length, but it may be remarked that the dimensions of the ossicles are liable to considerable variation according to the size of the particular example examined:—

	mm.
Scaphium.	
Length of ascending process, including the condylar process	3
Total length of the spatulate process, including its root	2·5
Length of the stapulate process, not including its contracted root, but only the concavo-convex portion which closes the external atrial aperture	2
Maximum width of the spatulate process	1
Interossicular Ligament.	
Length	1·2
Intercalarium.	
Length of the ascending process	4
Length of the horizontal process	3
Tripus.	
Total length not including curvature of the crescentic process	8
Length of anterior process	4
Length of the crescentic process, not including its curvature	4
Length of the articular process	2
Claustrum.	
Length	3·5

The Saccus Paravertebralis.—The free portion of the tripus, that is to say, the articular and anterior processes, with the posterior half of the interossicular ligament, and the horizontal process of the intercalarium, are situated within the cavity of a thin-walled fibrous sac—the "saccus paravertebralis" of WEBER. The sac extends from near the external atrial aperture of its side along the lateral surfaces of the centrum of the first vertebra and the anterior third of the complex centrum as far backwards as the insertion of the crescentic process of the tripus into the dorsal wall of the air-bladder, at which point its walls blend with the dorsal edge of the transverse membrane. The anterior wall of the sac is perforated by the inter-ossicular ligament as the latter process passes inwards from the anterior extremity of the tripus to its connection with the scaphium. In the Cyprinoid Fishes the cavity of the sac is in open communication anteriorly with the cranial cavity through the external atrial aperture and the foramen occipitale laterale (hypoglossal foramen). In *Macrones*, and probably in all Siluroid Fishes, on the contrary, the small size of the hypoglossal foramen, which is but sufficiently large to transmit the hypoglossal or first spinal nerve, and the complete closure of the external atrial aperture by the spatulate process of the scaphium, effectually prevent any communication between the cranial cavity and the saccus.

The cavity of the sac is occupied by a semi-gelatinous fluid, often partly oleaginous from the presence of an abundance of oil-globules, and contained within the meshes of a delicate fibrous network. The jelly-like material is nevertheless sufficiently liquid not appreciably to hamper the grosser movements of the various ossicles that are imbedded in it.

The roots of the first four pairs of spinal nerves traverse the cavity of the saccus where also their union to form the main trunks takes place. The ganglia on the dorsal roots of the nerves are likewise contained within the sac.

The Air-Bladder.—On examining the external surface of the body behind the pectoral girdle and dorsad to the origin of the pectoral fin a well-defined area of skin, generally slightly wrinkled or flaccid in spirit-preserved specimens, sometimes extremely tense, but always differing in appearance from the rest of the smooth scaleless skin, may be readily recognised on each side (fig. 15, *l.c.a.*). These areas we propose to call the lateral cutaneous areas. Each area is bounded by, and more or less firmly attached to, the stem of the post-temporal and the upper portion of the clavicle in front; the posterior process of the clavicle and the free dorsal edge of the ventro-lateral muscles below; and the distal margins of the expanded transverse processes, with the first rib, above and behind. The lateral line canal crosses the upper margin of each area a little below the dorsal attachment of the latter to the modified transverse processes. On reflecting either cutaneous area the great dorsolateral and ventro-lateral muscles of the body wall are seen to diverge at its posterior boundary, the former passing upwards and forwards over the expanded transverse processes to their insertion anteriorly into the posterior face of the skull, the latter passing downwards and forwards to their insertion into the ventral moiety of the clavicle (fig. 16). Between these divergent muscles the lateral wall of the anterior third of the air-bladder bulges outwards, and, normally, is very closely applied to the inner surface of the lateral cutaneous area of its side. The cutaneous areas are somewhat thinner than the rest of the skin, and their flaccidity, due perhaps to their greater thinness, combined with their intimate relations to the thin-walled air-bladder, renders it, as a rule, an easy matter to localize these areas without having recourse to dissection. In not a few Siluroids, as we shall subsequently have occasion to point out, in which the body is greatly compressed, and the cutaneous areas and the adjacent lateral walls of the air-bladder exceptionally thin, this part of the body appears partially translucent when the fish is held up to the light.

When the ventral wall of the body with the stomach, liver, and intestines have been removed the air-bladder comes into view as a flattish conical organ, broad in front, but somewhat narrower and more rounded behind (fig. 17, *a.b.*). The dorsal surface of the anterior third of the bladder is closely moulded to the shape of the ventral surfaces of the modified transverse processes of the fourth and fifth vertebræ, and to the keeled ventral surfaces of the complex and fifth vertebral centra, but for the posterior two-thirds of its length the bladder is much less closely related to the succeeding vertebral centra, transverse processes, and ribs, and lies comparatively free in the abdominal cavity. In front the lateral portions of the anterior wall of the air-bladder are firmly buttressed by the concave posterior faces of the bony structures formed by the post-temporal plates in conjunction with the crescentic extremities of the modified transverse processes of the fourth vertebra (figs. 3, 17, 18, *pt.p.*, *tp.*^{4}*a.*). The lateral walls of the anterior third of the bladder are in close relation with the inner surfaces of the lateral cutaneous areas, but more posteriorly the side walls contract from the external skin and the lateral musculature of the trunk, and, with the posterior wall, become closely embraced by the lateral and median posterior lobes of the mesonephros (fig. 18, *mph.*).

Immediately in front of the air-bladder, and closely moulded to the convexity of its anterior wall, the so-called head-kidney,[*] consisting of two lateral lobes and a thin transversely disposed connecting lobe, may be seen through the thin peritoneal layer which invests its ventral surface. Each lateral lobe occupies a recess between the inferior limb of the post-temporal in front, and the anterior division of the transverse process of the fourth vertebra behind, with its dorsal surface in contact with the floor of the membranous sac (saccus paravertebralis) in which certain of the Weberian ossicles are contained (figs. 17 and 18, *mph.r.*). The connecting lobe stretches transversely across the ventral surfaces of the body of the first vertebra and the adjacent portion of the basioccipital. The anterior surface of the gland is convex, and is closely invested by a strong transversely disposed aponeurotic membrane.

The peritoneum (fig. 23, *p.*) invests only the ventral surface of the air-bladder, extending laterally on to the side walls of the abdominal cavity, but in the medio-ventral line forms an incomplete mesentery, and is subsequently reflected on to the dorsal surface of the stomach; anteriorly, it is continued forwards from the ventral surface of the bladder over the corresponding surface of the "head kidney," and, after blending with what we shall subsequently refer to as the "aponeurotic membrane," is reflected backwards on to the dorsal surface of the œsophagus. Near the antero-lateral regions of the air-bladder the peritoneum by a characteristic reduplication forms on each side a deep cæcal pouch, with a somewhat restricted communication with the general peritoneal cavity, which extends outwards towards the inner surface of the proximal half of the clavicle and the root of its posterior process. These peritoneal cul-de-sacs exist in all Siluroid Fishes, and invariably contain prolongations of the lateral lobes of the liver. Their formation appears to be due to the unusual lateral extension of the anterior third of the air-bladder and the abutment of its outer walls against the inner surfaces of the lateral cutaneous areas, the partial displacement of the lateral hepatic lobes from their normal position between the air-bladder and the side walls of the body, which this modification involves, being compensated for by the outward and forward protrusion of a portion of each lobe into special peritoneal pouches. The position and relations of these pouches as well as the recesses for the "head kidney" are shewn in *Auchenoglanis biscutatus* (fig. 44, *p.c.s.*, and *mph.r.*).

Internally to its peritoneal coat the air-bladder is partially invested by a membrane which is obvious enough where it is in relation with what, for the present, we may call the proper anterior wall of the bladder, but in most instances is extremely difficult to trace elsewhere. In the former position it exists as a thin, but fairly strong, inextensible, and transversely-disposed fibrous membrane which is co-extensive with, and closely applied to, the mesial portion of the anterior wall of the bladder between the two post-temporal plates, and, although intimately applied to both, separates the bladder from the "head-kidney" in front. Laterally, on each side, the membrane is firmly attached to the ventral and inner margins of the post-temporal plate, and to the crescentic distal extremity of the transverse process of the fourth vertebra, blending with the ligamentous fibres by which these skeletal elements are rigidly connected together. The dorsal edge of the membrane is firmly attached to nearly the whole length of the anterior margins of the transverse processes in question, and towards the median line blends with the floor of each saccus paravertebralis. In the median line the dorsal margin appears to be continuous posteriorly with the fibrous floor of the aortic canal, and, on each side of the complex centrum becomes firmly attached to its oblique lateral ridge and to the radial nodule, while posteriorly a slip of fibres curves upwards and backwards to an insertion into the anterior or inner extremity of the dorsal lamina. The latter slip and the fibrous floor of the aortic canal are all that we could definitely identify as representing this membrane on the dorsal surface of the air-bladder. Traced ventrally the membrane suddenly becomes extremely thin, but, nevertheless, may be detected as extending for a short distance on to the lateral and ventral walls of the anterior portion of the air-bladder, where, however, it soon becomes lost as a definite structure, either by blending with the proper wall of the bladder, or becoming indistinguishable from the connective tissue by which the latter is connected with its peritoneal investment.

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[*] Otherwise the anterior lymphoid expansion formed by the fusion of the right and left halves of the mesonephros.

In close relation with the anterior face of the "head-kidney" there is a second transversely disposed aponeurotic membrane which occupies the same transverse plane on the dorsal side of the œsophagus as the pericardial septum on the ventral side, and is also attached laterally to the distal ends of the modified transverse processes and to the adjacent margins of the post-temporal plates, blending with the ligamentous fibres by which the transverse processes and the post-temporals are firmly united together, and also with the corresponding attachments of the first-mentioned membrane, but remains separated from the latter mesially by the "head-kidney." Ventrally, the aponeurosis blends with the peritoneum as the latter is reflected backwards from the under surface of the "head-kidney" on to the dorsal surface of the œsophagus. Dorsally, the membrane extends backwards as an investment to the dorsal surface of the "head-kidney" and the ventral faces of the basioccipital, the inferior limb of the post-temporal, and the body of the first vertebra, finally becoming inserted into the anterior margins of the modified transverse processes of the fourth vertebra, and there to some extent blends with the similarly attached dorsal edge of the preceding membrane. The aponeurotic membrane has clearly no relation to the air-bladder, but may be regarded simply as a dorsal and backward extension of the same fibrous sheet which, ventrally, separates the pericardial and abdominal cavities.

With regard to the first-mentioned of the two membranes it is not easy to decide in what light it should be regarded. In some respects it resembles a backward extension of the aponeurotic membrane. RAMSAY WRIGHT (43) in his description of the skeletal attachments of the anterior part of the air-bladder in *Amiurus catus*, evidently regards it as a portion of the proper anterior wall; at all events he describes the dorsal wall of the anterior chamber as being anteriorly attached to an oblique ridge on each side of the complex centrum, and to the thickened anterior margin of the transverse process of the fourth vertebra, and the only portion of the air-bladder that answers to this description is the transversely-disposed membrane in connection with the proper anterior wall. MCKENZIE (23) refers to it as an aponeurotic membrane separating the "head-kidney" from the air-bladder. On the other hand, we have but little doubt that the membrane described by SÖRENSEN (37) as more or less completely investing the air-bladder in certain Siluroids, and often becoming much thicker anteriorly than elsewhere, is identical with the one now under discussion. SÖRENSEN, however, apparently regards the membrane as constituting an inner layer of the peritoneal coat, although from his account it would seem to furnish a much more complete investment to the bladder than the outer layer, which carries the cœlomic epithelium, and is restricted solely to the ventral surface. For our own part we incline to the opinion that the membrane in question owes its existence as a definite structure to a delamination of the proper anterior wall of the air-bladder, which has also affected, but less obviously, the adjacent lateral, ventral, and dorsal walls, and ought, therefore, to be regarded as an integral portion of that organ. It is also more closely adherent to the proper wall of the air-bladder than to the investing peritoneum, and in some Siluridæ is much more obvious than in others, being traceable for a greater distance on to the lateral and ventral walls. In *Arius* and some other Siluridæ, in addition to the membrane now under consideration, which is also present, a second layer, anatomically and histologically undoubtedly a portion of the anterior wall of the bladder, may separate dorsally from the inner portion of the wall, and acquire skeletal attachments similar in almost every respect to those of the former. It is perhaps a matter of no great importance which view be taken, but from a physiological point of view the membrane is of some interest, inasmuch as its extensive attachments to rigid portions of the axial skeleton render it an efficient and unyielding buttress to the proper anterior wall of the bladder. As we shall frequently have occasion to refer to the extension of ossified deposit from adjacent skeletal structures into this membrane, more especially in the Siluridæ abnormales, we shall in future refer to it as the "superficial coat" of the air-bladder, distinguishing, however, that portion of it which specially buttresses the proper anterior wall as the "transverse membrane."

After the removal of its ventral wall the cavity of the air-bladder is seen to be divided by a characteristic T-shaped arrangement of two principal internal septa, one of which is transverse and the other longitudinal, into three main compartments. Of these compartments one is anterior and transversely disposed, and the other two lateral or posterior in position, and longitudinally arranged (fig. 18). The anterior chamber (*a.c.*) forms about one-third, and the two lateral chambers (*l.c.*) the remaining two-thirds of the antero-posterior extent of the bladder. The transverse septum (*t.s.*) is much the thicker of the two principal septa and divides the anterior chamber from the two lateral compartments, which, in turn, are separated from each other by the median longitudinal septum (*l.s.*). The longitudinal septum is continuous in front with the posterior face of the transverse septum, and both are continuous by their dorsal and ventral edges with the corresponding walls of the air-bladder. The transverse septum is not quite vertical, but inclines forwards from its dorsal to its ventral margin, the latter being more anteriorly situated than the former, but this statement more especially applies to the mesial portion of the septum. Hence, as in fig. 18, the transverse septum has its ventral margin somewhat V-shaped, with the apex pointing forwards, while the obliquity of the septum causes the two lateral compartments to slightly overlap the anterior chamber when viewed from the ventral surface. Along its ventral edge the transverse septum is almost co-extensive with width of the air-bladder, but dorsally the septum contracts from the lateral walls, so as to leave on each side an arch-like opening through which the anterior chamber communicates with each of the two lateral compartments. There is no communication between the lateral chambers except indirectly through the anterior chamber. In addition to the principal transverse and longitudinal septa there are three or four secondary transverse septa in each of the lateral compartments, which gradually diminish in width from before backwards (fig. 18, *t.s.'*). Each secondary septum, like the principal transverse septum, is of greater width dorsally than it is ventrally, and stretches from the longitudinal septum outwards towards the lateral or outer wall of the compartment, but before arriving at that point terminates in a deeply concave arch-like free margin. Dorsally as well as ventrally, the secondary septa are continuous with the corresponding walls of their respective compartments, and round their free margins the smaller cavities into which they subdivide each lateral chamber communicate with one another and with the anterior chamber. The principal transverse septum is really but the most anterior of these septa, although it differs from them in several important particulars, and notably in the firm attachment of its dorsal edge to the skeleton. In addition to the septa already mentioned, numerous buttress-like ridges of fibres arise from the dorsal and ventral margins of the longitudinal and the primary and secondary transverse septa and extend, root-like, into the adjacent roof and floor of the lateral compartments, thus still further adding to the sacculated or camerated structure of these chambers. With the exception of a few fibrous ridges that pass from the ventral margin of the anterior face of the primary transverse septum and blend with the adjacent ventral wall of the anterior chamber, the latter has perfectly smooth walls and is entirely devoid of ridges, sacculations, or septa.

The ductus pneumaticus (fig. 17, *d.p.*) communicates with the cavity of the anterior chamber by an opening situated in the median line of the ventral wall and close to the ventral edge of the primary transverse septum. The duct is not straight but somewhat sigmoid, with secondary flexions near its junction with the œsophagus.

As we have previously pointed out, the dorsal wall of the anterior chamber is closely related to the under surfaces of the expanded transverse processes of the fourth and fifth vertebræ, and also to the subvertebral keel which the complex and fifth vertebral centra, with their investing superficial ossifications, combine to form (fig. 23, *a.b.*). In fact the median portion of the dorsal wall, as far posteriorly as the primary transverse septum, is deeply grooved externally by the impression of the subvertebral keel, and this inpushing of the dorsal wall, which is visible internally as a prominent mediodorsal ridge, to some extent constricts the anterior chamber into two laterally bulging halves, while the vertex of the Λ-shaped transverse septum has the effect of continuing this constriction into the posterior wall of the chamber (figs. 18 and 23). On the other hand, the lateral compartments lie comparatively free in the abdominal cavity, or at all events are only related laterally and dorsally to the musculature of the body wall, the slender transverse processes and ribs, and to the mesonephros, but in no way are they attached to, or protected by, any special outgrowths or modifications of the skeleton as is the case with the anterior chamber.

The dorsal anterior and posterior walls of the anterior chamber are not only more or less intimately related to certain characteristic modifications of the axial skeleton but they are directly attached thereto at certain special points. But before referring to the skeletal attachments of the anterior chamber we may, with advantage, briefly describe the general arrangement of the principal sheets of fibres that form the walls of the air-bladder. Omitting the peritoneal investment on its ventral surface, and its superficial coat, the walls of the air-bladder are composed, as in all other Teleostei, of two principal layers of fibres, viz. :—the tunica interna and the tunica externa. The former consists of an extremely thin fibrous layer, supporting on its inner surface an epithelium of flattened cells, and furnishes a complete and continuous inner lining to the various primary and secondary cavities of the air-bladder, of uniform structure and thickness throughout. In specimens that have been preserved for any length of time in spirit, or have undergone maceration for a shorter period, the tunica interna readily separates from the tunica externa. In all the figures of the interior of the air-bladder which illustrate this paper the tunica interna has been removed so as to show the disposition and skeletal attachments of the fibres composing the outer tunic. After the removal of the inner tunic, and the exposure of the tunica externa, the free edge of the oblique ventral ridge of tripus, and the ventral surfaces of the heel-like process and of the posterior portion of the crescentic process of that ossicle, are clearly distinguishable on each side of the air-bladder, imbedded in the dorsal wall of the anterior chamber near its anterior extremity and a little to the outer side of the complex centrum (figs. 18 to 20). The tunica externa is always much thicker and consequently more rigid than the tunica interna ; it is, in fact, entirely owing to the thickness and strength of the former coat, combined with its more or less extensive attachments to the skeleton, that the air-bladder never collapses, even after its walls have been perforated, or portions removed, but invariably retains its normal shape and outline.

The tunica externa consists of two principal strata of fibres, an outer in which the general direction of the fibres is in the main longitudinal without being constant for all parts of their course; and an inner stratum composed of fibres with a general tendency to a transverse arrangement. The fibres composing either stratum, although they may vary their course and direction in different portions of the air-bladder, from longitudinal becoming oblique or nearly transverse, and *vice versâ*, and may describe various curves, very rarely coincide in direction at any one point, the fibres of one stratum crossing those of the other at more or less of a right angle. This characteristic arrangement is always fairly obvious in the anterior, lateral, and dorsal walls of the anterior chamber, and in the dorsal and lateral walls of the lateral compartments, where the two strata can be readily separated and the component fibres traced, but becomes more obscure in the ventral wall; there the fibres of the outer stratum pursue a somewhat irregular course and betray a tendency to interlace with one another, so as to be only traceable with some difficulty. As a rule it is only when the two strata approach their common attachments to rigid or moveable parts of the skeleton that their respective fibres exhibit a tendency to coincide in direction. In the walls of the lateral compartments, at all events in so far as the dorsal and ventral walls are concerned, the fundamental disposition of their fibres is to some extent obscured by the extension into them of the fibres composing the longitudinal septum, the primary and secondary transverse septa and their buttress-like ridges. In the septa themselves the component fibres are always vertical.

The series of semi-diagrammatic figures, 19–22 inclusive, are intended to illustrate the arrangement and skeletal attachments of the physiologically more important fibres of the outer and inner strata of the dorsal wall of the anterior chamber as seen from the interior, and also to some extent the corresponding features of the anterior, posterior, and lateral walls. In all cases it may be presumed that the ventral wall of the bladder and the whole of the tunica interna have been removed. In figs. 19 and 20, the inner stratum of the tunica externa is shown on the right side, and the fibres forming the outer stratum on the left side. In figs. 21 and 22 the insertions of the fibres of the outer and inner strata, respectively, into the crescentic processes of the tripodes are represented.

The disposition of the principal sheets of fibres in the tunica externa of the anterior chamber and their respective attachments to fixed or moveable portions of the skeleton are as follows:—

(1.) *Attachments to rigid portions of the skeleton.*

(*a.*) The posterior wall of the chamber, that is, the primary transverse septum, is composed of two vertically arranged strata of fibres, a posterior thin stratum, which dorsally and ventrally is continued into the dorsal and ventral walls respectively of the two lateral compartments, and a much thicker anterior stratum. Traced dorsally the component fibres of the latter stratum separate on the ventral face of the fifth vertebral centrum into two thick diverging sheets which pass dorsally, one on each side of the centrum, and, at the same time, curve slightly forwards into the dorsal wall of the anterior chamber; eventually, after separating from the rest of the dorsal wall, the fibres of each sheet become firmly inserted, from the median line outwards, into the ventral surface and obliquely along the sides of the centrum in question, and into the ventral surface of the transverse process of the fourth vertebra (figs. 19–20, *p.p.*). The line of attachment of each sheet coincides with the ridge-like dorsal margin of each superficial ossification and the posterior margin of the dorsal lamina, which, as we have previously described, form by their convergence anteriorly a characteristic Λ-shaped ridge (fig. 3). As these divergent sheets of fibres firmly attach the whole extent of the dorsal margin of the posterior wall to the axial skeleton, and physiologically must have the effect of preventing any distension or contraction of the anterior chamber in the posterior direction, they may not inaptly be termed its "posterior pillars."

(*b.*) If the fibres of the anterior layer of the transverse septum which form the posterior pillars by their dorsal attachment to the skeleton are traced ventrally instead of dorsally, they will be found to curve forwards into the ventral wall of the anterior chamber, where they assume a direction which varies according as they are mesially or more laterally situated, and, at the same time, represent the inner stratum of the tunica externa of this region. The more mesial fibres pursue a straight course forwards in the median line of the ventral wall, and ultimately curve upwards into the mesial portion of the anterior wall, where they form a vertically disposed stratum of fibres, and also blend with the corresponding portion of the outer stratum of the tunica externa, the fibres of which are also more or less vertically arranged. Beneath the anterior third of the complex centrum the confluent mesial portions of the two strata split into two slightly divergent bundles of fibres, which pass dorsally, one on each side of the centrum, to the ventral surface and sides of which, and to the radial nodules, they become closely adherent, leaving, however, a slip of fibres from each bundle to be continued dorsally to an insertion into the ventral ridge of the tripus (figs. 19 and 20, *a.p.*). As these bundles probably have much the same physiological significance with regard to the anterior wall that the posterior pillars bear to the posterior wall, and, by reason of their attachments to the complex centrum, render the anterior wall incapable of partaking in any enlargement or contraction of the anterior chamber, they may be designated the "anterior pillars." Their rigid skeletal attachments are not so extensive as in some other Siluridæ (*e.g.*, *Arius*), but, taken in conjunction with the transverse membrane and the post-temporal plates, they are obviously competent to prevent any forward bulging of the anterior wall. As we shall subsequently point out, the more laterally situated fibres of the inner stratum of the tunica externa of the ventral wall pursue an oblique course forwards, outwards, and upwards, and are then traceable into the antero-lateral and lateral wall of each half of the chamber; from thence they converge in the corresponding half of the dorsal wall, in the form of a broad triangular sheet, to their ultimate attachment to the tripus. The fibres of the *outer* stratum of the tunica externa in the mesial portion of the anterior wall, if traced ventrally from the anterior pillars and their skeletal attachments, become easily separable from those of the inner stratum, and ultimately extend into the ventral wall, where they assume a direction which, in the main, is longitudinal or oblique; but this arrangement is somewhat modified by their tendency to describe curves and loops, and to become interwoven with one another. It is worthy of note that the attachments of the anterior and posterior pillars to rigid portions of the skeleton will not only render the anterior chamber inexpansible in the direction of its antero-posterior axis, but will also tend to limit, even if it does not entirely prevent, any expansion ventrally, inasmuch as the longitudinally-arranged fibres which form the inner layer of the tunica externa in the mesial portion of the ventral wall are directly continuous between the two pillars, and also share their respective skeletal attachments. In not a few Siluroids (*e.g.*, *Arius*) these longitudinal fibres are unusually strongly developed, and form either a single ridge or a pair of ridges, which project from the median line of the ventral wall into the cavity of the chamber, and anteriorly and posteriorly are directly continuous with the anterior and posterior pillars.

(*c.*) Over a somewhat lozenge-shaped area in the median portion of the dorsal wall of the anterior chamber, bounded in front and behind respectively by the anterior and posterior pillars, and laterally by the oblique posterior margins of the two triangular sheets which constitute the lateral portions of the dorsal wall, the tunica externa becomes so extremely thin as to allow the subvertebral keel to be readily seen through it when the tunica interna has been removed (figs. 19 and 20). Although extremely thin in this region the tunica externa is not free, but, on the contrary, is firmly adherent, like a periosteum, to the under surface and sides of the complex centrum and part of the body of the fifth vertebra, its area of attachment exactly coinciding with the extent of the superficial ossifications that invest the centra. It is scarcely necessary to mention that apart from the adhesion of the medio-dorsal portion of the anterior chamber to the skeleton, the close investment of the lateral portions of the dorsal wall by the expanded transverse processes of the fourth and fifth vertebræ must preclude all possibility of expansion or contraction in that direction.

(2.) *Attachments to moveable ossicles.*

(*a.*) The fibres forming both strata of the tunica externa in the lateral and antero-lateral walls of the anterior chamber converge as they pass into their respective halves of the dorsal wall towards the point a little to the outer side of the complex centrum, and there become inserted into the crescentic process of the tripus. The fibres constituting the inner stratum in these regions are vertically arranged; traced thence into the ventral wall they pass more or less obliquely backwards, and eventually are traceable into continuity with the more laterally situated of the fibres which form the posterior pillars, and consequently have the same rigid skeletal attachments as the latter. Traced dorsally from the antero-lateral and lateral walls the fibres converge in each half of the dorsal wall towards the crescentic process of the tripus (figs. 18, 20, 21, *in.st.*). The fibres derived from each antero-lateral wall are inserted, at first into the outer margin of the ventral ridge of the tripus, and more posteriorly into the outer margin of the crescentic process and the apex of its heel-like projection. The fibres derived solely from each lateral wall have their final insertions from before backwards into the hinder margin of the heel-like process, and into the whole extent of the posterior margin of the crescentic process. From an inspection of figs. 18 and 19 it will be apparent that the convergence of these transversely or rather obliquely arranged fibres in each half of the dorsal wall to their connection with the corresponding tripus causes the greater part of the dorsal wall of the chamber to present the appearance of being formed of two broad and well-defined triangular sheets of fibres, with the apex of each sheet connected with the tripus of its side, and the broad base continued outwards into the antero-lateral and lateral walls. Reference to the same figures will also show that the oblique posterior margins of the two sheets slightly overlap the skeletal insertions of the posterior pillars into the dorsal lamina.

The fibres forming the outer stratum of the tunica externa in the lateral and antero-lateral walls (figs. 19, 20, 22, *o.st.*) if traced into the dorsal wall also converge towards the corresponding tripus, and, in so doing, form the outer of the two strata of which each triangular sheet is composed. For the latter part of their course, that is, as they approach the tripus, these fibres coincide in direction with the corresponding fibres of the inner stratum (compare figs. 19 and 20, *o.st.*, *in.st.*). Eventually their inner extremities, like the analogous fibres of the inner stratum are successively inserted from before backwards into the oblique ventral ridge, the heel-like projection, and the posterior margin of the crescentic process of the tripus (figs. 20, 22, *o.st.*). The insertion of these fibres into the different regions of the crescentic process, although practically identical with the corresponding insertions of the fibres of the inner stratum, is, of course, external to the latter. Traced outwards from either tripus the precise course which the fibres of the outer stratum pursue varies somewhat according to their points of insertion into that ossicle. The most anterior fibres, that is, those starting from the anterior end of the ventral ridge, after traversing the anterior part of the dorsal wall curve downwards into the antero-lateral wall, and finally extend into the ventral wall, where their disposition is mainly longitudinal or oblique (fig. 19). The bulk of the fibres, however, as they successively pass from the regions of the tripus already indicated, on reaching the antero-lateral and lateral walls loop backwards, and in doing so describe a characteristic curvature, the convexity of which is directed towards the ventral surface, and the concavity towards the dorsal surface, and then, as they are traced backwards, extend into the lateral, and finally into the dorsal wall of the lateral compartment of that side (fig. 19, *o.st.*). The most posterior of the fibres, that is, those that are attached to the posterior margin of the crescentic process, describe a very similar curvature, but in this instance, in the dorsal wall itself, the convexity of the curve being directed outwards and the concavity inwards, and subsequently pass into the dorsal wall of the neighbouring lateral compartment, there becoming obliquely arranged with regard to the long axis of the chamber (fig. 19). In nearly all parts of their course the curvilinear fibres of the outer stratum cross those of the inner stratum at a greater or less angle, and only coincide with the latter in direction as they both approach their attachments to the tripodes. It is obvious that all fibres that ultimately become inserted into the moveable tripodes at one extremity of their course are at the opposite extremity absolutely or relatively fixed, either as is the case with those forming the inner stratum of the tunica externa, through their direct continuity with the posterior pillars, or, as with those forming the outer stratum, through their extension into the walls of the inexpansible posterior or lateral chambers of the air-bladder. The specialisation of the dorsal wall of the anterior chamber to form special tracts of fibres in the form of two broad and stout triangular sheets, separated from each other by a thin skeletally attached medio-dorsal area, each of which is composed of two intersecting strata of fibres, and extends outwards from its attachment to the tripus to form the lateral and antero-lateral walls, where it becomes intimately related to the inner surface of the adjacent lateral cutaneous area, is extremely characteristic not of *Macrones* only but of nearly all other normal Siluridæ.

(*b.*) That portion of the tunica externa which occupies the concavity of the crescentic process of each tripus is specialized to form a series of tightly stretched fibres connecting that process with the radial nodule. The fibres are firmly inserted into the nodular prominence at the dorsal extremity of the radial nodule, and from that point radiate outwards and are eventually attached to the inner margin of the ventral ridge and the whole extent of the inner concave edge of the crescentic process (figs. 19 to 22, *r.f.*). The prominence on the radial nodule occupies, as it were, the centre of a circle of which the crescentic process itself forms a large arc, and the fibres in question, like the radii of a circle, converge from the process to the nodule. For these fibres we would suggest the term "radial fibres." A thin layer of tunica interna invests the ventral surface of the crescentic process as well as the inner surface of the nodular prominence, but without forming any special attachment to either; the removal of the layer, which can be readily effected, at once exposes the surfaces of both ossicles.

Although, as we have previously pointed out, the typical disposition of the fibres of the two strata of the tunica externa is transverse or circular for the inner stratum and longitudinal for the outer, it is obvious that this arrangement has been widely departed from in particular portions of the bladder. Thus, while the disposition of the fibres of the inner stratum in the lateral and anterior walls of the anterior chamber exhibits but a slight modification of the transverse arrangement, in the dorsal wall, on the contrary, the fibres become more or less oblique, and in the ventral wall oblique or even longitudinal. On the other hand, the fibres of the outer stratum, although somewhat irregular in their course, are mainly longitudinal in the ventral wall, but oblique in the dorsal and anterior walls, and curvilinear in the lateral. It is the specialization of particular tracts of fibres for the attachment of the walls of the air-bladder to fixed or moveable skeletal elements that is mainly responsible for the many marked deviations from the normal arrangement.

Broadly speaking, it may be concluded that in *Macrones* the air-bladder consists of two physiologically distinct portions, a posterior, including the two lateral compartments, which from its septate or camerated structure can have but little capacity for change of volume in the way of distension, and an anterior chamber which is obviously capable of such volumetric variations. And also that any variations in the capacity of the anterior chamber can only be produced by lateral bulging or contraction in which the anterior, posterior, dorsal, and ventral walls have no share. It may further be concluded that as the fibres of the lateral and antero-lateral walls of the chamber are directly inserted into the tripodes at one extremity while remaining actually or relatively fixed at the other, any lateral variations of its internal capacity must impart corresponding movements to the tripodes and to the remaining Weberian ossicles.

As regards the histological structure of the air-bladder we have nothing to add to MACULLUM's description of *Amiurus* (24), which agrees substantially with that previously given by LEYDIG (22) for other Siluridæ. We can also confirm in the case of *Macrones* MACULLUM's statement as to the absence of muscular fibres in the walls of the bladder of *Amiurus*.

In many Teleostei specially developed retia mirabilia or "vaso-ganglia," invested by a special modification of the epithelium of the tunica interna, are present, usually in the form of conspicuous flesh-coloured projections into the cavity of the air-bladder. Neither in *Macrones* nor in any other Siluroid that we examined were these structures present; and we are able to confirm MACULLUM's statement (*loc. cit.*) that the epithelium presents no special or local modifications where it invests the capillary plexuses.

The Relations of the Spinal Nerves to the Anterior Vertebræ and the Weberian Ossicles.—The mode of exit of the anterior spinal nerves from the neural canal, as well as their peripheral distribution, are substantially the same as described by RAMSAY WRIGHT in the case of *Amiurus catus* (42), but on one interesting point with reference to the relations of the roots of the third spinal nerve to the intercalarium, which has an important bearing on the exact homology of that ossicle, *Macrones* differs from *Amiurus*. Owing to the absence of an ascending process in the intercalarium and the generally reduced condition of that ossicle in the latter Siluroid, RAMSAY WRIGHT was unable to satisfy himself as to its exact relations to the nerve in question, and consequently missed an important item of confirmatory evidence in support of the view originally suggested by BAUDELOT, and subsequently adopted by

NUSBAUM, GRASSI, and himself, that the intercalarium is identical with the neural arch of the second vertebra.

The foramen for the first spinal, or "hypoglossal" nerve, traverses the exoccipital, and is seen internally just over the roof of the cavum sinus imparis (fig 5, *sp.n.'*), but externally is visible immediately in front of the external atrial aperture (figs. 1, 4, and 9, *sp.n.'*). The dorsal and ventral roots of the second and third spinal nerves traverse distinct paired foramina in the fibrous wall of the neural canal between the neural plate of the exoccipital in front and the arch of the third vertebra behind. The roots of the second nerve pass outwards between the ascending processes of the scaphium and intercalarium, the foramen for the dorsal root being situated near and a little behind the upper extremity of the scaphium, and the one for the ventral root at a much lower level (figs. 4 and 5). The foramina for the roots of the third nerve lie comparatively close together between the ascending process of the intercalarium and the arch of the third vertebra (figs. 4 and 5). The roots of the fourth spinal nerve pass outwards from the neural canal through a single foramen in the anterior part of the arch of the third vertebra (*sp.n.*^{4}) ; those of the fifth nerve through a pair of foramina near the posterior margin of the arch of the fourth vertebra (*sp.n.*^{5}) ; and similarly the roots of the sixth nerve through a pair of apertures in the posterior part of the arch of the next vertebra; and so on with the succeeding anterior spinal nerves (fig. 2).

As the roots of the first to the fourth spinal nerves, inclusive, emerge from the neural canal to pass to their peripheral distribution, they traverse the cavity of the saccus paravertebralis on the dorsal side of certain of the Weberian ossicles. The hypoglossal nerve crosses the interossicular ligament, and emerges from the saccus between the inferior limb of the post-temporal and the opisthotic plate of the exoccipital, and immediately behind the vagus. The second and third nerves cross the anterior process of the tripus, and leave the saccus between the inferior limb of the post-temporal and the anterior division of the transverse process of the fourth vertebra. The fourth nerve emerges from the posterior extremity of the saccus, and, after passing dorsad to the crescentic process of the tripus, is continued by its ramus ventralis along the ventral surface of the transverse process of the fourth vertebra. The rami ventrales of the two succeeding spinal nerves traverse the dorsal surfaces of the transverse processes of the fourth and fifth vertebræ respectively. As the rami ventrales of the fourth to the sixth spinal nerves, inclusive, pass to their peripheral distribution, they curve round the dorsal and lateral surfaces of the anterior chamber of the air-bladder, and, in the latter part of their course, lie on each side between the lateral cutaneous area and the lateral wall of the bladder.

The ventral divisions of the first to the fourth spinal nerves, inclusive, are distributed to the muscles of the pectoral arch and fin, and those of the fifth and sixth to the lateral musculature of the trunk.

SAGEMEHL (33) has described an additional spinal nerve as emerging from the neural canal between the claustrum and the ascending process of the scaphium in *Silurus glanis*. On this point we can only say that after a most careful examination we have utterly failed to satisfy ourselves that any such nerve exists in *Macrones*. RAMSAY WRIGHT (44) states that he has been equally unsuccessful in detecting this nerve in *Amiurus catus*.

Other Species of Macrones.

Of the remaining species of *Macrones* recorded in the 'British Museum Catalogue,' we have examined the following :—*M. planiceps, M. nigriceps, M. gulio, M. tengara, M. Wolffii, M. micracanthus, M. Hoevenii,* and *M. aor*. We also dissected a species labelled *M. armatus*,* but which we were unable to identify with certainty as belonging to any of the species referred to in the 'British Museum Catalogue,' or elsewhere. With the exception of the last-mentioned, the locality of which was unknown, all these species are East Indian, collectively ranging from India eastwards through Burmah, Siam, Java, Sumatra, and Borneo.

With the exception of *Macrones aor* the variations met with in the structure of the air-bladder are perhaps of no great importance, but nevertheless merit a brief reference from the fact that they illustrate the nature and extent of the modifications that may occur in the normal species of the same genus, and *Macrones* is one of the very few genera of which we have been able to examine a fairly representative series of species.

M. planiceps and *M. armatus* very closely resemble *M. nemurus*. The same remark applies also to *M. nigriceps, M. gulio, M. tengara,* and *M. Wolffii,* except that the lateral compartments of the air-bladder in these species have comparatively undivided cavities, there being but slight rudiments of two or three secondary transverse septa in each. The post-temporal plates may also vary slightly in the depth of their posterior concavities. In *M. micracanthus* all traces of secondary transverse septa have entirely disappeared. In *M. tengara* the lateral cutaneous areas are rendered very evident externally by circular patches of black pigment, and, as GÜNTHER (15) remarks, these ocellus-like patches are more conspicuous in young than in old specimens. In *M. Wolffii* the walls of the bladder are somewhat thicker than in any other species of *Macrones*, and the lateral compartments relatively smaller. In *M. Hoevenii* the post-temporal plates are unusually expanded, and form rounded or somewhat oval laminæ of bone, thin, brittle, and cancellous at their edges, but much thickened towards the centre of their anterior faces, where each is perforated by a tubular socket for the head of the clavicle. The posterior face of each plate is much more concave than is the case with any of the preceding species, and, as in *M. nemurus*, the concavity is still further deepened round its inner and ventral margins by the unusually long and slender crescentic portion of the transverse process of the fourth vertebra, the two structures together forming on each side a concave bony surface, which is closely applied to the adjacent antero-lateral wall of the bladder. The latter organ is proportionally larger than in other species of the genus, but the cavities of its lateral compartments are much more broken up and sub-divided through the greater development of secondary transverse septa and their buttress-like ridges.

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* This specimen was given to us by Dr. DAY.

The modifications initiated in *M. Hoevenii* are carried to an extreme degree in *M. aor.* In this species each post-temporal plate instead of being merely concave on its posterior face, as in *M. Hoevenii*, becomes curiously bullate and goblet-shaped, with the mouth directed backwards and the much contracted stem continuous with the inferior limb (fig. 25, *pt.p.*). Although the mouth of the bulla is directed backwards, its cavity, which gradually contracts, seems to extend inwards as an excavation in the inferior limb, nearly as far as the articulation of the latter with the basioccipital. The crescentic distal extremity of the modified transverse process encircles and strengthens the ventral and inner lips of the mouth of the bulla, and is firmly attached thereto by ligament. From the antero-lateral angles of the anterior chamber of the air-bladder two cæcal diverticula are given off, which are just sufficiently large to extend into and fill the cavities of the two bullæ. The diverticula are composed of both tunics of the bladder, but the tunica externa is extremely thin. With the exception of the antero-lateral cæca the walls of the air-bladder are much thicker than is usual in *Macrones.* The ventro-lateral margins of the anterior chamber are curiously thickened internally by strong rib-like aggregations of the vertical fibres of the inner stratum of the tunica externa, which separate a series of small slit-like sacculi. The cavities of the lateral compartments are partially obliterated by the excessive development of the secondary transverse septa and their buttress-like bundles of fibres, as well as by the growth of vertically disposed fibrous columns extending between their dorsal and ventral walls. Marginal bundles of fibres are also developed in connection with the lateral walls of these compartments, and extend inwards in the form of incomplete septa; the latter, with the smaller buttresses which they give off, to a large extent obliterate the lateral passages by which the compartments normally communicate in front with the anterior chamber. The lateral walls of the anterior chamber are not in direct contact with the superficial skin, the two structures being more or less completely separated by the anterior lobes of the mesonephros, but in general structure, and in the relations and attachments of its fibres to fixed or moveable portions of the skeleton, this section of the air-bladder presents no special peculiarities. The Weberian ossicles are almost precisely similar to those of *M. nemurus.* The ascending process of the intercalarium, relatively to the horizontal process, is rather stouter than usual, the latter being extremely thin and slender, and, moreover, is forked at its outer extremity where imbedded in the interossicular ligament. As in several other Siluroids, the posterior wall of the atrial cavities is strengthened by a small median process of bone, apparently derived from the posterior and dorsal margin of the basioccipital, but more probably due to the ossification of the median portion of the fibrous wall itself. The process is grooved on its posterior face, and the groove receives the vertical ridge of fibrous tissue which imperfectly separates the two cavities.

Bagrus bayad.

In the structure of the air-bladder and in the general details of its osteology this African Siluroid differs in no essential respect from *Macrones nemurus.* Relatively to the size of the body the air-bladder is somewhat smaller than in the latter species, and, with the exception of a single short but stout secondary transverse septum in each of its lateral compartments, has smooth walls and undivided cavities. The walls of the bladder are moderately thick, but somewhat thinner in the lateral and antero-lateral regions than elsewhere. The tripus has no heel-like process, and the intercalarium has a well-developed ascending process in addition to a horizontal one.

Bagrus docmac.

In a skeleton of this species in the British Museum we noticed that the post-temporal plates were incompletely ossified, a deep cleft extending inwards from their outer margins.

Chrysichthys macrops.

In a skeleton of this Siluroid in the British Museum collection the anterior margin of each of the transverse processes of the fourth vertebræ was bent sharply downwards so as to form a vertical, transversely disposed plate which must have excluded the post-temporal plate from contact with the anterior wall of the air-bladder.

Pseudobagrus brachysoma.

In this Siluroid there are several noteworthy peculiarities of the skeleton in which it differs from most of the preceding species.

The stem and inferior limb of the post-temporal (fig. 26, *pt.s.*, *pt.i.*) are no way modified to form the post-temporal plate which is so characteristic of the various species of *Macrones* and *Bagrus.* On the contrary the stem is vertically cleft into an inner and an outer process, and the cleft with its groove-like prolongation forms an articular cavity (*cl.s.*) for the proximal extremity of the clavicle, the latter being retained in position by strong ligamentous fibres which convert the groove into a tubular socket. The transverse process of the fourth vertebra is so deeply cleft that its divergent anterior and posterior divisions ($t.p.^4a.$, $t.p.^4p.$) are but slightly united at their roots, and would resemble normal transverse processes but for their greater length and thickness. The posterior division ($t.p.^4p.$) is directed obliquely backwards, and has its root connected by a thin lamina of bone with the corresponding portion of the succeeding transverse process. The anterior division ($t.p.^4a.$) is unusually stout, with a broad flat root, which is in relation by its ventral surface with the tripus, but flattened from before backwards for the remainder of its length. It has but a slight downward curvature, and, instead of being prolonged into a crescentic distal portion, as in *Macrones*, has its thick truncated extremity firmly applied to the inner moiety of the cleft post-temporal stem in such a way as to deepen the articular groove for the clavicle by strengthening its inner margin, and at the same time entirely excludes the post-temporal from contact with any portion of the anterior wall of the air-bladder. From this arrangement it will follow that the transverse processes alone furnish the usual bony buttresses for the antero-lateral regions of the bladder, in addition to affording a firm and rigid support to the pectoral girdle. At their junction the post-temporal and transverse process are firmly united together by ligament. A transverse membrame stretches between the distal extremities of the anterior divisions of the modified transverse processes, in close relation with the proper anterior wall of the bladder, and elsewhere has the same skeletal attachments as in *Macrones.*

The air-bladder has fairly thick walls, and is subdivided in the usual way into an anterior and two lateral compartments. Relatively to the anterior chamber, the lateral compartments are somewhat larger than is usually the case, and extend backwards in the abdominal cavity as far as the origin of the seventh pair of ribs. The primary transverse septum is exceptionally narrow, and forms a stout column of vertically disposed fibres. The longitudinal septum is incomplete posteriorly, so that the two lateral chambers communicate with each other directly, as well as indirectly, through the anterior compartment. There are no secondary transverse septa, and both the anterior and lateral compartments have smooth non-sacculated walls. In all other points the air-bladder closely resembles that of *Macrones nemurus.*

The outer surface of each lateral cutaneous area is rendered very conspicuous by a large circular patch of black pigment, surrounded by a white margin.

The Weberian ossicles are also very similar to those of *Macrones;* the tripus, however, has no heel-like process. The relative lengths of the anterior and crescentic processes of this ossicle are 8 mm. and 6 mm. respectively, instead of being approximately equal.

The posterior wall of the atria sinus imparis is strengthened by a spicular upgrowth from the dorsal margin of the hinder face of the basioccipital, as in *Macrones aor.*

Pseudobagrus fulvi-draco.

The skeleton, air-bladder and Weberian ossicles of this species are precisely similar to those of *P. brachysoma.*

Liocassis micropogon.

In this and the next species (*Bagroides melanopterus*) we meet with a reversion to the *Macrones* type.

In *Liocassis* there is a well developed post-temporal plate, with a concave posterior face, and a thickened and convex anterior surface. To the ventral and inner margins of each plate the crescentic extremity of the anterior division of the transverse process of the fourth vertebra is applied, precisely as in *Macrones*. The air-bladder closely resembles that of *Pseudobagrus*, but relatively to the size of the body, is, perhaps, somewhat smaller, the reduction, however, being mainly at the expense of the lateral compartments. Both the anterior and lateral chambers have undivided cavities and perfectly smooth walls. The primary transverse septum is represented by a stout vertical column of fibres, continuous behind with the longitudinal septum, and having its dorsal margin attached to the skeleton in the usual fashion. The longitudinal septum is complete posteriorly.

The tripus has but the barest rudiment of a heel-like process, but in all other points the Weberian ossicles are in close agreement with those of the type form.

Bagroides melanopterus.

This species is to some extent intermediate between *Liocassis micropogon* and *Macrones Hoevenii*. In the nature of its skeletal modifications *Bagroides* closely resembles the latter, but as regards its air-bladder the agreement is with *Liocassis;* nevertheless, *Bagroides* has one or two noteworthy peculiarities of its own.

Each post-temporal plate is unusually large, and extends inwards along the lower border of the inferior limb—with which, of course, it is continuous—nearly as far as the articulation of the latter with the basioccipital. In shape the plate is a somewhat irregular oval, the long axis of which is directed from within outwards and downwards. The posterior face of the plate is deeply concave, resembling a shallow cup; its peripheral margins are extremely thin and brittle, but towards the centre of its anterior face the plate becomes greatly thickened, and is at the same place perforated by a tubular and vertically-disposed socket for the proximal end of the clavicle. The crescentic distal extremity of the modified transverse process is much shorter than in *Macrones*, but has the same relations to the ventral and inner margins of the correlated post-temporal plate as in the latter Siluroid, or, more particularly, as in *M. Hoevenii.* At the junction of the crescentic process with the much thicker root of the transverse process there is a deep groove, which is concave from above downwards, and looks forwards and a little outwards; and into this groove is received a rounded articular ridge on the posterior face of the inferior limb of the post-temporal, near the junction of the latter with the post-temporal plate. The interlocking articulation of the two structures enables the transverse process to afford an exceptionally firm support to the shoulder-girdle. The ligament described and figured in *Macrones nemurus* as passing between the transverse process and the post-temporal plate, although present in most of the species so far described, is absent in *Bagroides.*

The air-bladder is somewhat pyriform in shape, with the broad end directed forwards, and has thicker and more rigid walls than usual. In the smoothness of its inner surface, and in the total absence of all trace of secondary transverse septa, as well as in the narrow column-like shape of the primary transverse septum, the air-bladder very closely resembles that of *Liocassis.* A short tubular cæcum is attached to the posterior end of the bladder, and has its cavity subdivided into two lateral canals by a corresponding backward prolongation of the longitudinal septum, which separates the two lateral compartments anteriorly. The two canals are distinct from each other, but communicate with their respective lateral chambers in front. In the general structure of the walls of the anterior chamber, and in the relations and attachments of their principal sheets of fibres to fixed parts of the skeleton and to the tripodes, *Bagroides* exhibits no perceptible difference from *Macrones.* We have described the walls of the air-bladder as being thicker and more rigid than usual, but this statement does not accurately apply to the antero-lateral regions of the anterior chamber, for there the walls are extremely thin over definitely circumscribed areas exactly co-extensive with the post-temporal plates. In each area the wall of the bladder appears to be formed mainly, if not exclusively, by the vertically disposed fibres of the inner stratum of the tunica externa, with the addition of the extremely thin tunica interna. Both areas bulge forwards into the concavities of their respective post-temporal plates.

The Weberian ossicles are very similar to those of *Macrones,* except that the heel-like process of the tripus is of unusual length, being, in fact, as long as the posterior or inwardly-curved segment of the crescentic process. The intercalarium has tolerably stout ascending and horizontal processes.

Rita crucigera.

This species, so remarkable for the enormous size of its pectoral and dorsal spines, which in a specimen less than twelve inches long were four and a half and three inches in length, respectively, and proportionally massive, very closely resembles *Pseudobagrus brachysoma* in most of the osteological details with which we are now concerned.

The decurved anterior division of the transverse process of the fourth vertebra is somewhat shorter than usual but very massive. Its distal half is flattened from before backwards, and, anteriorly, is firmly applied to the relatively slender inferior limb of the post-temporal, to the entire exclusion of the latter from contact with any portion of the anterior wall of the air-bladder. The distal portion of the process is not produced into a crescentic prolongation but somewhat abruptly ceases at the point where it forms the inner margin of the articular groove for the clavicle. The altogether exceptional thickness of these processes is obviously correlated with the equally exceptional development of the pectoral spines and the girdle which supports them. The superficial ossifications investing the complex and fifth vertebral centra agree in the extent of their growth with those of *Macrones nemurus*. The oblique lateral ridges of the complex centrum are but feebly developed, and each ridge is directly continuous with the dorsal lamina of its side. The radial nodule is a short but thick ossification, firmly attached, but not anchylosed, to about the centre of the confluent lateral ridge and dorsal lamina. The stem and ascending process of the post-temporal together form a broad granulated plate which is freely exposed on the surface of the body, near the postero-lateral angle of the skull. The posterior process of the clavicle (fig. 27, *cl.p.*) is unusually long and broad, and extends backwards to about the level of the second rib; its upper margin is slightly concave, and coincides with the inferior limit of the lateral cutaneous areas of its side.

The anterior chamber of the air-bladder (fig. 27, *a.c.*) has the normal size relatively to that of the body, but the lateral compartments (*l.c.*) are very imperfectly developed, although they have the usual relations to the former, and are separated from each other by a short, stout, longitudinal septum (*l.s.*). The primary transverse septum (*t.s.*) is somewhat contracted but extremely thick, and its dorsal edge has an extensive attachment to the lateral surfaces of the centrum of the fifth vertebra and to the ventral surfaces of its transverse processes. The anterior wall of the bladder is firmly buttressed by the anterior divisions of the modified transverse processes (*t.p.*^{4}*a.*), and externally to this, in the antero-lateral regions, by the concave inner surfaces of the clavicle and its posterior process. Apparently by way of compensation for the small size of the lateral chambers, two comparatively thin-walled cæcal diverticula are given off from the postero-lateral regions of the anterior chamber, which extend backwards, one on each side of the abdominal cavity nearly as far as the anus (fig. 27, *c.dv.*). These diverticula are simple cæca, tubular in shape, and of fairly uniform calibre throughout, but communicating with the anterior chamber by wide funnel-shaped mouths, situated at the outer side of the apertures whereby the same compartment opens into the two rudimentary lateral chambers. The cavities of the cæca are simple and undivided. In a brief reference to the air-bladder of this species, DAY (9) describes the right cæcal diverticulum as usually passing over to the left side, and then curving across the commencement of the left one, while the latter at first passes backwards and is then sometimes curved on itself, but in the only specimen at our disposal the cæca pursued a fairly straight course backwards towards the anus, and finally bent slightly inwards towards each other. With the exception of these cæcal outgrowths the walls of the air-bladder are exceptionally thick, but nevertheless retain their normal attachments both to fixed portions of the skeleton and to the moveable tripodes. It will be noticed, however, that the dorsal attachments of the lateral portions of the primary transverse septum are to the ventral surfaces of the transverse processes of the fifth vertebra, instead of, as in *Macrones*, to those of the fourth vertebra, and it is apparently due to the backward shifting of these attachments that the posterior pillars lose their direct insertion into the posterior margins of the dorsal laminæ.

Of the Weberian ossicles, the tripus and the scaphium are for the most part perfectly normal; the intercalarium, however, has neither ascending nor horizontal processes, and, in fact, is represented only by a small nodule of bone imbedded in the middle of the interossicular ligament. The tripus (*tr.c.*) has no heel-like process, and its anterior extremity is somewhat thickened for the attachment of the stout interossicular ligament. In correlation with the exceptional thickness of the walls of the air-bladder the crescentic process, and its ventral ridge, are more stoutly developed than in most of the preceding types.

Akysis variegatus.

We have only been able to examine solitary examples of the two rare species, *Akysis variegatus* and *Acrochordonichthys pleurostigma*, and it unfortunately happened that both specimens were too badly preserved to admit of our results being otherwise than incomplete. We regret this the more because it is obvious that in these species both the air-bladder and the skeleton, and especially the former, differ considerably from the more normal types of those structures that we have so far described. As our specimen of *Akysis* was slightly the better preserved of the two, we shall deal with it first.

The centrum of the first vertebra is a thin discoidal bone completely excluded from view on the ventral surface by the forward extension of the superficial ossifications. The complex and fifth vertebræ are rigidly connected together, and as firmly united to the skull by the superficial ossifications, which not only invest the lateral surfaces of their centra, but also extend forwards on to the ventral surface of the body of the first vertebra, and even slightly overlap the basioccipital. The sixth vertebra is quite free, and its transverse processes carry the first pair of ribs. The spine of the third vertebra is represented by a thin lamina of bone, the dorsal margin of which slopes downwards towards the skull, and articulates by a serrated suture with a descending process derived from the supraoccipital spine. The spinous process of the fourth vertebra is exceptionally massive, and cleft distally for the support of the first two interspinous bones of the dorsal fin. The transverse process of the fourth vertebra is not only greatly expanded, but its anterior and posterior margins are somewhat decurved so as to form the anterior and posterior boundaries of a shallow concave recess on the ventral side of the process (fig. 29, *t.p.*^{4}). The anterior margin is much thicker and more strongly decurved than the posterior, especially towards its outer extremity, where, in addition, it curves slightly backwards. The remainder of the process is comparatively thin and somewhat triangular in shape, with the apex directed outwards. The decurved anterior portion, and the thin triangular lamina respectively represent the usual anterior and posterior divisions into which this transverse process is normally divided. The corresponding process of the fifth vertebra is more strongly developed than its successors, with a slight forward inclination and a pointed distal extremity, but confluent at its broad base with the root of the preceding process (*t.p.* 5).

Superficial ossifications greatly thicken the ventro-lateral margins of the complex and fifth vertebral centra, and there form well-marked longitudinal ridges; they are also produced ventrally and enclose between them a fairly conspicuous groove for the dorsal aorta (fig. 29, *a.g.*). Near the hinder extremity of the complex centrum each longitudinal ridge is produced slightly outwards into a short triangular process (fig. 29), which is clearly a rudimentary representative of the very similar, but much more pronounced ventral process of *Bagarius* and *Glyptosternum*, and, like the latter, has its origin from a ridge-like thickening of the superficial ossification. We could detect no trace of an oblique lateral ridge in connection with the complex centrum, but a dorsal lamina is on each side represented by a thin slender spicule of bone which becomes detached from the ventral surface of the modified transverse process at a point a little behind, and to the inner side of, the distant extremity of the crescentic process of the tripus, and, after passing downwards, inwards, and a little forwards, ventrad to the cardinal groove, terminates in a free extremity close to the lateral surface of the complex centrum, or rather is connected with the latter by a fibrous extension only (fig. 29, *d.l.*). The groove for the posterior cardinal vein is very evident on the right side, between the thickened ventro-lateral edges of the complex and fifth centra and the ventral surfaces of the roots of the contiguous transverse processes. In the region of the dorsal lamina, it is obvious that, as usual, the groove is almost completely encircled by bone. On the left side the groove is inconspicuous.

The ascending process, and the stem of the post-temporal (*p.t.*) together form an expanded plate of bone at each of the postero-lateral angles of the skull, which covers the epiotic and articulates in the usual way with the pterotic in front, and the supra-occipital above. The inferior limb (*pt. i.*) is very slender, and has but a slight forward inclination as it passes inwards to join the basioccipital (*b.o.*). Its outer extremity firmly articulates with the recurved distal end of the anterior division of the modified transverse process, and the two, in conjunction with the inner surface of the post-temporal stem, combine to form a deep articular groove for the proximal extremity of the clavicle (*cl.*).

The air-bladder is represented by two laterally-situated and somewhat ovoid, thin-walled sacs, each of which occupies the concavity of the bony recess, formed by the modified transverse process of its side* (fig. 30, *a.s.*). There is no trace of lateral compartments, or of any connection between the two sacs otherwise than by a thin solid stratum of fibres, which extends transversely between the two, and in the median line is firmly adherent to the ventral surface of the complex centrum; neither could we detect any trace of a ductus pneumaticus. The anterior and posterior walls of each sac seemed to be closely attached to the corresponding margins of the bony recess, in which the sac itself is partially enclosed, while the inner wall is similarly adherent to the lateral surface of the complex centrum, to the triangular ventral process, and to the dorsal lamina. The rigid skeletal attachments of the two air-sacs are substantially similar to those of the similarly modified air-bladders of *Bagarius* and *Glyptosternum*, and, probably, as we shall point out more particularly in our description of the last-mentioned genus, are capable of strict comparison with the attachments of a normal anterior chamber, or, at least, present only such differences as are necessitated by the constriction of the bladder into two distinct lateral divisions. Although obvious enough elsewhere, we could detect no definite disposition of fibres in the dorsal wall of either of the two air-sacs, neither could we trace the usual convergence of fibres from the antero-lateral and outer walls towards the crescentic process of the tripus; in fact the dorsal wall of both sacs appeared to be represented solely by an extremely thin stratum of connective tissue. We are inclined to regard this stratum as belonging to the inner tunic, the tunica externa of the dorsal wall having completely atrophied. We were unable to discover any trace of an investing epithelium, but failure in this respect was probably due to the ill-preserved condition of the specimen. It is, of course, possible that the apparent degeneration of the proper fibrous portion of the dorsal wall may also be the result of the same cause, but from the undoubted existence of similar structural lesions in other abnormal Siluridæ we prefer, provisionally at any rate, to regard this condition as normal so far as *Akysis* is concerned.

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* In a specimen three and a half inches in length, each air-sac was 3·5 mm. long and 2·7 mm. in width.

The possibility that structural defects in the connection of the walls of the air-bladder with the tripodes might be correlated with the existence of similar retrogressive modifications in those portions of the internal ear which are specially associated with the Weberian mechanism, induced us to make a careful examination of the cavum sinus imparis and its contents. The cavum itself and its atrial diverticula appeared to be perfectly normal, but relatively small in point of size. A ductus endolymphaticus was present, but of a sinus endolymphaticus we could find no trace whatever. How far our inability to discover the latter structure was due to the condition of the specimen, or to its real absence, we are unable to say, but while admitting the possibility of the former alternative, we must point out that the latter receives some support from the almost certain suppression of the sinus in other and in many respects similarly abnormal Siluridæ.

Of the Weberian ossicles the scaphium has no ascending process, but is otherwise normal; its condyle is at the hinder extremity of the spatulate process, which, anteriorly, has the usual relations to the external atrial aperture of its side. The intercalarium is reduced to a very small nodule, imbedded in the interossicular ligament, having lost both its ascending and horizontal processes. We could find no trace of claustra. The tripus is a triradiate and very slender ossicle (fig. 29, *tr.*). The anterior process is directed forwards and a little inwards as it passes to its connection with the scaphium; the crescentic process, on the contrary, is directed backwards and slightly outwards, and, instead of curving inwards towards the complex centrum, remains in a straight line with the anterior process, and rapidly tapers to an acutely pointed distal extremity. At the junction of the two processes, and on the inner side of the ossicle, a long and slender articular process is given off, which also tapers to a point and ultimately fits into a deep pit on the lateral surface of the anterior portion of the complex centrum. The crescentic process of each tripus occupies the same relative position with regard to the inner portion of the degenerate dorsal wall of the corresponding air-sac that it does in each of the lateral halves of the anterior chamber of a normal air-bladder, with its inner margin directed towards the ligamentous connection of the dorsal lamina with the side of the complex centrum. The radial fibres of the tripus appear to be represented by a few scattered fibres derived from the dorsal edge of the inner wall of each air-sac and inserted into the inner margin of the crescentic process.

Akysis Kurzii, DAY.

DAY (9, pp. 703–4) describes a new species of *Akysis* from Pegue Yomas under this name. The air-bladder is said to be "small, in the abdominal cavity, not enclosed in bone," but the description is obviously too brief to allow of any comparison with *A. variegatus.*

Acrochordonichthys pleurostigma.

The only example of this interesting Javan species that we have been able to examine was about two inches in length, and, unfortunately, in an even worse state of preservation than our solitary specimen of *Akysis.* So far, however, as we were able to determine, *Acrochordonichthys* closely resembles *Akysis*, both in the condition of the air-bladder, and in the nature of the modifications which the anterior vertebræ and their processes undergo.

The transverse processes of the fourth vertebra (fig. 28, *t.p.*^{4}) are greatly expanded and enclose on each side on their ventral surfaces shallow concave recesses, each of which is separated from its fellow of the opposite side by the somewhat compressed centrum of the complex vertebra. The anterior margin of each recess is strongly decurved, the posterior and other margins but very slightly so. The free distal extremity of the anterior margin is somewhat produced and recurved. The transverse process of the fifth vertebra (*t.p.*^{5}) resembles those of the succeeding rib-bearing vertebræ, and forms no part of the bony recesses for the air-sacs. The lateral ridge of the complex centrum and the corresponding dorsal lamina form a feebly developed but continuous ridge extending along the side of the centrum obliquely upwards, backwards, and outwards towards the ventral surface of the root of the modified transverse process. We could find no trace of the usual lateral grooves for the posterior cardinal veins, or of the ventral outgrowths from the superficial ossifications which are so conspicuous a feature in *Bagarius* and *Glyptosternum*, and to a less extent in *Akysis* also.

The stem and ascending process of the post-temporal are very similar to those of *Akysis*. The inner surface of the stem forms the outer boundary, and the recurved distal portion of the modified transverse process the inner and anterior walls, of the socket for the head of the clavicle (*cl.*). There is no trace of an inferior limb, in fact, this process seems, as it were, to have been crowded out by the abutment of the anterior margin of the transverse process against the posterior and opisthotic plates of the exoccipital.

The air-bladder differs in no essential feature from that of *Akysis*, and, as in the latter Siluroid, is completely constricted into two small laterally placed air-sacs, which occupy the concavities of the modified transverse processes of the fourth vertebra (fig. 30, *a.s.*).* There is no communication between the two sacs, neither is there a ductus pneumaticus. As regards the skeletal attachments of the air-bladder, the degenerate condition of its dorsal wall, and the apparent atrophy of the sinus endolymphaticus, there is also an extremely close resemblance between the two genera, and this agreement further extends in almost every detail to the condition of the Weberian ossicles.

It must be admitted that while there are several features in connection with the air-bladder in *Acrochordonichthys* and *Akysis* which favour the belief that its structural peculiarities are due to the degeneration of an originally normal bladder, our results are not quite conclusive on this point. Mere reduction in the size of the air-bladder is obviously not sufficient to prove the uselessness of its connection with the auditory organ through the Weberian mechanism, but structural imperfections in either organ, or in the connecting ossicles, would be decisive. That the two air-sacs are distinct we have no doubt, and the total atrophy of the ductus pneumaticus seems equally certain, but more definite information as to the presence or absence of the sinus endolymphaticus, and as to the condition of the dorsal walls of the air-sacs and their relations to the tripodes, is desirable before it can be positively affirmed that the air-bladder and Weberian mechanism are physiologically useless in these genera. Our failure to find a sinus endolymphaticus may be due, as we have already pointed out, either to its absence, as we suggest, or to the imperfect preservation of our specimens, but if the former alternative be true, our tentative conclusions on other uncertain points would receive strong support, for if the physiological connection of the Weberian ossicles and the air-bladder were lost through the partial or complete atrophy of the dorsal walls of the air-sacs, it would be reasonable to anticipate the existence of similar retrogressive changes in that part of the auditory organ which is specially related to those structures. In subsequently dealing with two other abnormal Siluroids (*Bagarius* and *Glyptosternum*) we shall point out that they furnish strong confirmatory evidence in support of our provisional conclusions with regard to *Acrochordonichthys* and *Akysis.*

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* The dimensions of each sac were : length, 2·33 mm., width, 1·5 mm.

Olyra burmanica, DAY.

The air-bladder in this species is said by DAY (10, p. 711) to be "large, thin, and not enclosed by bone." Brief as this description is, it may be legitimately inferred that the air-bladder is of the normal Siluroid type.

Amiurus catus.

RAMSAY WRIGHT (41 and 42) has described not only the condition of the anterior vertebræ in the adult, but also their development in very young examples of this species. These vertebræ are figured as seen in a ventral view and in longitudinal vertical section (42, Plate IV., figs. 7–8). Various sections, horizontal and transverse, through the cranium, auditory organ, and the anterior vertebræ of young specimens (3–4 cm. in length) are also represented (*loc. cit.*, figs. 9–15), but no figures of the air-bladder or of its various skeletal attachments are given. We have dissected several examples of the species, and can confirm the accuracy of RAMSAY WRIGHT'S account so far as the adult Fish is concerned.

Both as regards its skeletal modifications and the structure of the air-bladder, *Amiurus* exhibits a general resemblance to *Pseudobagrus brachysoma.* The two species differ, however, in certain minor features. In *Amiurus* the centrum of the first vertebra is said to be provided with a pair of rudimentary transverse processes. The transverse processes of the fourth vertebra are somewhat more expanded than in *Pseudobagrus,* and their anterior and posterior divisions are less obviously distinct. The sixth vertebral centrum is not invested by superficial ossifications, and is therefore free. As is *Pseudobagrus,* there are no post-temporal plates.

The air-bladder is normal. The primary transverse septum is wider than in *Pseudobagrus.* There are no secondary transverse septa, and unlike *Pseudobagrus,* the longitudinal septum is complete posteriorly. The skeletal attachments of the bladder are essentially similar to those of *Macrones.* RAMSAY WRIGHT (*loc. cit.*) describes the anterior wall as attached dorsally to the ventral edge of the transverse process of the fourth vertebra; this attachment, however, is really the dorsal insertion of what we have hitherto called the transverse membrane into the anterior margin of the process, and does not implicate the proper anterior wall as in *Arius* and its allies.

The scaphium is normal, but the intercalarium has neither ascending nor horizontal processes, and is represented by a small osseous nodule in the interossicular ligament. The tripus is also normal, but is without the heel-like process so characteristic of this ossicle in *Macrones,* and many of the preceding types.

GROUP—PIMELODINA.

Platystoma tigrinum.

We have been able to examine two examples of this interesting South American form, one, a skeleton, about 2½ feet in length, now in the Zoological Museum of the Mason College, and the other a spirit-preserved specimen about 15 inches long. Our description of the skeleton applies more particularly to the larger of the two examples.

The series of rigidly interconnected anterior vertebræ includes the first, the complex and the fifth and sixth vertebræ, but the articulation of these vertebræ with the skull is of a somewhat more flexible character than is the case with most other Siluridæ. As compared with those of the normal free vertebræ which succeed them, the centra of the modified vertebræ, with the exception of that belonging to the first vertebra, are all greatly elongated, but less in girth, and more compressed than the former.

The centrum of the first vertebra (figs. 31 and 32, *v.*′) is exceptionally well developed, being nearly as large as any of the free centra, from which, however, it differs in the greater depth of its posterior concavity as compared with the shallow anterior concavity. It has no trace of transverse or of accessory articular processes. The complex centrum (*c.c.*) is greatly elongated and compressed laterally. Its anterior concavity is funnel-shaped, and the posterior almost tubular through its unusual depth. In the dry skeleton a cleft extends from the floor of the neural canal to about the centre of the anterior third of the complex centrum, and partially separates the anterior from the posterior tubular concavity (fig. 31); superiorly the cleft is continuous with a large foramen in the adjacent neural arch, through which the dorsal and ventral roots of the fourth spinal nerve emerge from the neural canal ($sp.n.^4$). We can hardly doubt that this cleft results from the imperfect coalescence of the bodies of the third and fourth vertebræ, and serves to indicate the line of union of the anterior concavity of the latter with the posterior concavity of the former. Neither the basioccipital nor the complex centrum develop accessory articular processes, but remain widely separated by the well-developed body of the first vertebra. The centrum of the fifth vertebra is a trifle longer than the complex centrum, but, like the latter, is much compressed; the condition of its anterior and posterior surfaces is, however, reversed, the anterior being deep and tubular, and the latter funnel-shaped and relatively shallow (fig. 31, $v.^5$). The centrum of the sixth vertebra is much shorter, although longer than the normal centra; anteriorly it is somewhat contracted, but widening behind it equals in the size the body of the seventh vertebra with which it articulates, like its predecessor it has the anterior cavity deeper than the posterior ($v.^6$). The seventh vertebra ($v.^7$) is normal and free. Although closely and firmly articulated together, no anchylosis takes place between the neural arches of any of the modified anterior vertebræ (fig. 31). The spinous processes of the third and fourth vertebræ are distinct and divergent, the former being directed obliquely forwards to its connection with the exoccipitals and supraoccipital, while the latter which is much the longer inclines obliquely backwards (fig. 31, *n.s.*^{3}, *n.s.*^{4}). The spine of the fifth vertebra is much shorter and inclines forwards and may abut against the posterior margin of the preceding spine (*n.s.*^{5}). The remaining spines are bifid and normal.

The transverse processes of the fourth, fifth, and sixth vertebræ are all more or less flattened and expanded, suturally articulating with one another by slightly serrated margins; their distal extremities are free, being separated by wide clefts. By the expansion and sutural union of these processes an unusually extensive wing-like lamina of bone is formed on each side of the anterior vertebræ, which is somewhat concave from before backwards and also from side to side, in conformity with the convex dorsal wall of the anterior chamber of the air-bladder (fig. 32). The transverse process of the fourth vertebra is the largest of the three, and distally is cleft into the usual anterior and posterior divisions (*t.p.*^{4}*a.*, *t.p.*^{4}*p.*). The anterior division (*t.p.*^{4}*a.*) is much thickened and, in addition, is slightly decurved at its free extremity so as to form a partial support to the lateral portions of the anterior wall of the bladder; anteriorly, the distal end of the process articulates by means of a roughened facet with the outer extremity of the inferior limb of the post-temporal, and also with the cleft stem of that bone, thus forming an incomplete posterior boundary to the socket for the head of the clavicle (fig. 34, *t.p.*^{4}*a.*). The posterior division is a broad thin horizontally disposed lamina. The transverse process of the fifth vertebra (fig. 32, *t.p.*^{5}) is nearly as large as the preceding process, the posterior division of which it very closely resembles. The transverse process of the sixth vertebra (*t.p.*^{6}), though more expanded than any which succeed it, is by far the smallest of the modified processes and carries the first rib (*r.*$'$).

A thick layer of superficial ossified deposit appears to invest the lateral and ventral surfaces of the anterior vertebral centra from the first to the sixth, inclusive, and also to extend laterally on to the adjacent ventral surfaces of the roots of all the modified transverse processes, thus converting the lateral grooves for the posterior cardinal veins into canals of exceptional length (fig. 32, *cd.c.*). Apparently as the result of the ventral growth of the ossifications round the dorsal aorta, the artery in this part of its course is completely enclosed within a bony canal (figs. 31 and 32, *a.c.*) which appears to burrow its way through the different centra, and opens anteriorly on the body of the first vertebra and posteriorly on the centrum of the sixth. The sutural lines between the modified transverse processes may be traced inwards on the superficial ossifications investing the different vertebral centra in the form of irregular wavy lines, which roughly indicate the position of the intervertebral sutures but without precisely coinciding therewith (fig. 32). The dorsal laminæ are represented on each side by a thin narrow process of bone (fig. 32, *d.l.*) which extends from the lateral surface of the anterior third of the complex centrum obliquely outwards and upwards to blend with the ventral surface of the root of the first of the modified transverse processes. Each lamina is situated ventrad to the corresponding posterior cardinal vein and indeed forms the inferior lip of the anterior opening of the bony canal through which the vein passes. At the ventral and anterior extremity of each dorsal lamina, and but partially confluent therewith, there is a large crescent-shaped radial nodule (*r.n.*). The lateral surface of the body of the fifth vertebra is traversed by a stout ridge which, commencing near the anterior end of the centrum, extends obliquely backwards and upwards, and eventually bends directly outwards on to the ventral surface of the transverse process (fig. 32). This ridge receives the dorsal insertion of the primary transverse septum of the air-bladder.

In the skull of *Platystoma* the neural plates of the exoccipitals are undeveloped, the lateral boundaries of the transversely oval foramen magnum being formed by the concave inner margins of the posterior plates. A stout process of bone projects directly backwards from each posterior plate, and from this process one of the two great compressor muscles of the air-bladder takes its origin. The posterior wall of the atria sinus imparis is strengthened in the median line by a small vertical column of bone which extends upwards from the dorsal edge of the posterior face of the basi-occipital and nearly meets the hinder margin of the roof of the cavum sinus imparis.

The air-bladder is well developed and extends backwards as far as the origin of the eighth pair of ribs (fig. 33, *a.b.*). In shape it is somewhat ovoid, being but slightly broader in front than behind. The lateral portions of its anterior wall are partially supported by the anterior divisions of the first pair of transverse processes (fig. 34, *tp.*^{4}, *a.*); posteriorly to this the outer walls are at first in contact for a limited extent with the lateral cutaneous areas, but subsequently separate from the skin and the lateral musculature of the body wall as they contract to enclose the relatively narrower posterior section of the bladder. A remarkably strong muscle has its insertion into nearly the whole extent of each half of the ventral wall of the anterior third of the bladder, and its fibres, gradually converging as they are traced forwards, curve round the anterior wall and pass dorsally between the inferior limb of the post-temporal and the transverse process of the fourth vertebra to their origin on the posterior plate of the exoccipital a little to the outer side of the foramen magnum (fig. 33, *cp.*, *m.*). As the contraction of these muscles must necessarily lead to the forcible compression of the anterior chamber of the bladder, and possibly to the expulsion of its gaseous contents, we shall in future refer to them as the "compressor muscles." A much smaller and hitherto undescribed muscle (*t.t.*) occupies the recess on each side of the centrum of the first vertebra, between the latter and the corresponding compressor muscle. This muscle also arises from the posterior plate of the exoccipital, but its fibres pass directly backwards, and are prolonged into a long and slender tendon, which is ultimately inserted into the anterior wall of the bladder in close proximity to the attachments of the latter to each radial nodule (figs. 33, 34, *t.t.*).

Internally the bladder is divided into spacious anterior and lateral chambers by strong primary transverse and longitudinal septa (fig. 34, *ts.*, *ls.*), while each lateral compartment is also sub-divided into a series of transversely arranged inter-communicating cavities by six incomplete secondary transverse septa (fig. 34, *ts.'*). Strong root-like bundles of fibres radiate from the dorsal edges of the secondary septa into the dorsal wall of the bladder, and still further contribute to the peculiar camerated structure of that organ. The lateral portions of the primary transverse septum remain nearly vertical, but its mesial part is inclined obliquely forwards before it finally becomes continuous with the ventral wall; hence the ventral edge of the septum is somewhat V-shaped, with the apex directed forwards, while the lateral compartments and the longitudinal septum which separates them are prolonged forwards for some distance ventrad to the inclined septum and to the anterior chamber.* The dorsal edge of the transverse septum is firmly inserted into the oblique ridges on the lateral surfaces of the centrum of the fifth vertebra, and also into their prolongations on to the ventral surfaces of the contiguous transverse processes (fig. 32).

The tunica externa of the anterior wall of the bladder is divisible into two strata, of which the outer and thicker is attached in the median line by its dorsal edge to the ventral and lateral surfaces of the anterior portion of the complex centrum, and also to the radial nodules and dorsal laminæ, but externally to this on each side the outer stratum, instead of extending into the dorsal wall and becoming connected with the corresponding tripus, separates from the inner and is inserted by its dorsal margin into the anterior edge and distal extremity of the transverse process of the fourth vertebra. In the lateral walls of the anterior chamber the fibres composing this stratum pursue the usual curvilinear course as they are traced into the dorsal wall, where they converge in the form of triangular sheets to their insertion into the convex outer margins of the crescentic processes of the tripodes (fig. 34, *tr.c.*, *o.st.*). The sheets are somewhat narrower than usual, and have a slightly concave inner margin, while the thin medio-dorsal area of the tunica externa, which invests and is attached to the ventral and lateral surfaces of the complex and fifth vertebral centra, is relatively much wider than in most other Siluroids; hence the surfaces of these centra and the roots of their transverse processes are readily seen through the thin area when the tunica interna has been removed. The inner and much thinner of the two strata of the tunica externa of the anterior wall divides in the median line beneath the complex centrum, and on each side the more mesially situated fibres are inserted dorsally into the inner margin and ventral surface of the root of the crescentic process of the tripus; laterally to this point the fibres of the inner stratum, which are vertically disposed, describe an inward curvature towards the tripus as they extend into the dorsal wall, and eventually become inserted into the convexity of its crescentic process (fig. 34, *in.st.*). From the antero-lateral and lateral walls of the anterior chamber the fibres of the same stratum may be traced into the dorsal wall, where they form a thin layer on the inner surface of the curvilinear fibres of the outer stratum but, instead of extending inwards to their usual insertion into the tripodes, thin away near the inner edges of the triangular sheets. The insertion of the tendon of each of the small extrinsic muscles of the bladder into the anterior wall of the anterior chamber exactly coincides with the position of those fibres of the inner stratum of the tunica externa, which are dorsally inserted into the inner margin of the root of the crescentic process of the tripus, and is in close contiguity with the similar insertion of the radial fibres of that ossicle. As the contraction of these muscles would probably have the effect of tightening such fibres, and, therefore, restrict the lateral movements of the tripodes, we venture to suggest for each the name of "tensor tripodis." The radial fibres of the tripus are strongly developed, but otherwise are normal.

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* In fig. 34 the right half of the transverse septum has been partially removed.

Apart from the outer stratum of the anterior wall of the bladder, which is dorsally attached to the complex centrum, to the radial nodules and to the dorsal laminæ, as well as to the transverse processes of the fourth vertebra, we could detect no equivalent to the transverse membrane of other Siluroids. It is possible, however, that the outer stratum includes, not only a portion of the tunica externa of the anterior wall, but the transverse membrane as well; at all events, such an explanation is suggested by the fact that the outer stratum has the characteristic attachment of the transverse membrane to the dorsal laminæ, which is, apparently, never the case with any portion of the proper tunica externa in other Siluroids. All the normal Pimelodinæ that we have examined resemble *Platystoma* in this respect.

A small cæcal appendage is closely attached to each of the lateral walls of the anterior chamber, and is partially overlapped by the great compressor muscle of its side (figs. 33 and 34, *al.c.*). The cavity of this curious appendage communicates with that of the anterior chamber by means of a number of slit-like apertures in the outer wall of the latter (fig. 34). Anteriorly, each cæcum separates from the wall of the bladder, and expands into a pear-shaped enlargement, which is in contact with the inner surface of the dorsal extremity of the clavicle. The cavity of the appendage is broken up into a series of intercommunicating spaces by a network of fibrous bundles, and the tunica interna is prolonged outwards from the anterior chamber through the slit-like orifices in its outer wall, so as to line the interior of the cæcum and the spaces enclosed by the fibrous network.

The claustra are well developed and lie one on each side of the foramen magnum; each ossicle is strongly curved in conformity with the shape of the aperture which it partially encircles. The scaphium has the usual shape, but its spatulate process is relatively small and greatly thickened; the ascending process is short and very slender. The intercalarium is represented by a thick nodule in the inter-ossicular ligament. The tripus also is normal in shape; its anterior process, however, is slightly longer than the crescentic process. The latter portion of the ossicle has a well-marked oblique ridge on the ventral surface of its root, and, in the larger of our two specimens was greatly thickened in addition to having its posterior margin traversed by a deep groove for the insertion of the fibres of the dorsal wall of the anterior chamber.

Excluding *Auchenoglanis*, *Platystoma* is a fairly representative type of the more normal Pimelodinæ, and for this reason a detailed account of the structure and relations of its air-bladder has been given. From this point of view the more noteworthy features in *Platystoma* are :—

(*a.*) The laxity of the articulation of the anterior vertebræ with the skull through the absence of accessory articular or subvertebral processes.

(*b.*) The presence of two pairs of extrinsic compressor and tensor tripodis muscles in connection with the air-bladder.

(*c.*) The absence of any definitely recognisable transverse membrane distinct from the skeletally attached outer strata of the lateral portions of the anterior wall of the bladder.

(*d.*) The tendency of the air-bladder to develope antero-lateral cæcal appendages.

In the extensive development of the superficial ossifications, and in the extent and character of the skeletal attachments of the anterior wall, as well as in some other minor features, *Platystoma* closely resembles the Arioid type, to which reference will subsequently be made.

Platystoma fasciatum and P. coruscans.

JOHANNES MÜLLER (28,* Plate 4, figs. 8, 9) has noted the presence of antero-lateral cæcal appendages in *P. fasciatum* similar to those of *P. tigrinum*, but in *P. coruscans*, if we rightly interpret his brief description of this Siluroid, such appendages are entirely wanting. The anterior vertebræ of *P. fasciatum* have been figured and described by SÖRENSEN (37, Plate 2, figs. 13, 14) from whose account it would seem that they do not in any important respect differ from those of *P. tigrinum*.

Sorubim lima.

Under the name of *Platystoma lima*, JOHANNES MÜLLER (*loc. cit.*) briefly refers to this Siluroid as not possessing the cæcal appendages so characteristic of the anterior chamber of the air-bladder in *P. tigrinum* and *P. fasciatum*.

Piramutana piramuta.

The anterior vertebræ and their modified transverse processes in this species are very similar to the corresponding structures in *Platystoma*. As in the latter genus the transverse processes of the fourth and fifth vertebræ on each side combine to form an extensive wing-like outgrowth with a decurved anterior margin which closely envelopes the dorsal wall of the anterior compartment of the air-bladder, and at the same time buttresses the anterior wall (fig. 35, *t.p.*^{4}*a.* and *t.p.*^{4}*p.*).

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* See section entitled "Zellige Schwimmblasen bei einigen Siluroiden."

The air-bladder itself is more distinctly cordâte than in *Platystoma*, and its walls are extremely thin (*a.b.*). The ventral wall of the anterior chamber is almost completely invested by powerful compressor muscles. A tensor tripodis is also present on each side, and has the same origin and insertion as in *Platystoma*. No anterolateral or other cæcal appendages are present. Two rudimentary secondary transverse septa only are present in each lateral compartment (*t.s.*′). In the general structure of the walls of the anterior chamber, and in their relations and attachments to the transverse processes of the fourth vertebra and to the tripodes *Piramutana* differs in no essential respect from *Platystoma*. The lateral walls of the anterior chamber are in close and extensive contact with the lateral cutaneous areas.

Piramutana Blochii.

Under the name of *Pseudariodes clarias* (BLEEK.) SÖRENSEN (36) figures and describes the air-bladder of this species. His figure (*l.c.*, Plate 3, fig. 45) shows the left compressor muscle and on the right side the cavity of the bladder and its internal septa.

Piratinga filamentosa.

JOHANNES MÜLLER (28) has figured and described the air-bladder of this Siluroid under the name of *Pimelodus filamentosa* (LICHTENST.). The organ is said to consist of two entirely distinct flat sacs lying one behind the other and both cellular throughout. The ductus pneumaticus is connected with the anterior sac. The posterior sac is said not to contain the usual central cavity, the whole of the interior being occupied by small air-cells. Later on (p. 141) in alluding to the same species, MÜLLER says, "in which there is a second cellular air-bladder, without any union with the first, without connecting duct, and without communication with a respirable medium."

Pimelodus maculatus.

In this species the air-bladder differs but little from that of *Piramutana*, and the same may be said of the skeletal modifications.

The air-bladder has rather thick walls, and, in addition to the primary transverse and longitudinal septa, there is a rudiment of a single secondary transverse septum in each lateral compartment. The lateral portions of the primary transverse septum are nearly vertical, and have their dorsal margins attached to the ventral surfaces of the transverse processes of the sixth vertebra, but, as they approach the median line, they become inclined obliquely forwards towards the ventral surface of the bladder, while their dorsal margins curve forwards parallel to each other along the sides, and eventually along the ventral surface of the fifth vertebral centrum, to which they become firmly attached. Near the anterior end of the centrum the lateral halves of the septum unite at an acute angle in the median line, and form a forwardly inclined keel projecting into the cavity of the anterior chamber, and partially subdividing it into two lateral divisions. The anterior portion of the longitudinal septum makes a slight deviation from the median line, and unites with the posterior face of the left half of the primary transverse septum; hence it is that the right lateral compartment extends forwards between the opposed faces of the converging lateral halves of the transverse septum until the latter finally unite in the median line anteriorly. These features are more or less characteristic of other species of *Pimelodus* with normal air-bladders (*vide P. ornatus*, fig. 36) and of *Piramutana*, but they are particularly well marked in *P. maculatus.*

The divergence of the dorso-lateral and ventro-lateral muscles of the trunk is so slight that scarcely any portion of the lateral walls of the anterior chamber is in contact with the external skin, and the two structures are further separated by a considerable amount of fatty tissue.

In an immature specimen of this species about 4 inches in length, the air-bladder had extremely thin walls, and its anterior chamber was in close and extensive relations with lateral cutaneous areas, which externally presented the appearance of superficial blisters of the skin. The longitudinal septum was attached in front to the right half of the primary transverse septum instead of the left, and hence the right lateral compartment was prolonged forwards on the dorsal or posterior face of the inclined septum, between its converging lateral halves.

A compressor and a tensor tripodis muscle were present in relation with each half of the anterior chamber.

Pimelodus ornatus.

In this species also the air-bladder and anterior vertebræ are essentially similar to those of *Piramutana.*

The anterior wall of the bladder (fig. 36) is somewhat emarginate in the median line, and consequently the anterior chamber presents the appearance of two subglobose sacs continuous with each other across the median line, and with the two lateral compartments posteriorly. Relatively to its length and width, the bladder, and especially its anterior chamber, are somewhat deeper than in *Piramutana.* Its walls are extremely thin. Two pairs of secondary transverse septa (*t.s.'*) are present, as also are compressor and tensor tripodis muscles.

Pimelodus pulcher, BOUL.

Our examples of this species formed part of the collection of Fishes made by the late Mr. CLARENCE BUCKLEY, at Canelos, in Western Ecuador, and subsequently described by Mr. G. A. BOULENGER in the 'Proc. Zool. Soc. of London,' for 1887, p. 274. As both the air-bladder and certain portions of the skeleton exhibit some interesting deviations from the normal type, a more detailed notice of this species will be given.

The first, the complex, and the fifth vertebræ are more or less rigidly connected together by the usual means, the sixth being the first that is freely moveable (fig. 39, *v.'*, *c.c.*, *v.*^{5}, and *v.*^{6}). The body of the first vertebra is very small. The complex centrum is nearly twice the length of the fifth centrum, and this again is somewhat larger than any that follow. The ventro-lateral edges of the complex and fifth centra are thickened by a continuous deposit of superficial bone, which, however, does not extend ventrally or laterally so as to convert the grooves for the dorsal aorta (*a.g.*) and posterior cardinal veins into complete bony canals. The cardinal grooves are rather deep and, as usual, that on the right side is more conspicuous than the left one. Radial nodules are attached to the lateral surfaces of the complex centrum, and from each nodule a slender dorsal lamina (*d.l.*) is continued obliquely backwards and upwards, ventrad to the corresponding cardinal groove, along the posterior margin of the transverse process of the fourth vertebra, with which the lamina eventually fuses.

The expanded transverse processes of the fourth vertebra (*t.p.*^{4}) have broad flat roots, but are strongly decurved along their anterior margins and produced distally into slender recurved processes, which form the inner walls of the sockets for the clavicles; to the decurved anterior margin of each process the inferior limb of the post-temporal (*pt.i.*) is closely applied. The posterior portion of the process is nearly flat, but terminates distally in a pointed projection. The ventral surface of each transverse process will therefore form a shallow, transversely-disposed recess, which is slightly concave from before backwards, except for a short distance at its root. The transverse process of the fifth vertebra (*t.p.*^{5}) is quite free, and much longer than the normal rib-bearing processes.

The air-bladder is partially constricted into two ovoid, laterally-situated sacs (figs. 39 and 40, *a.s.*), which occupy the concave recesses furnished by the modified transverse processes of the fourth vertebra (*t.p.*^{4}*a.*), and are in free communication with each other through a narrow tubular portion passing from one to the other across the ventral surface of the complex centrum.* This intermediate tubular portion is connected by a persistent ductus pneumaticus with the œsophagus. There is no trace of lateral compartments. As regards its rigid skeletal attachments and the relations of its component fibres to the tripus, each air-sac is strictly comparable to the lateral half of an anterior chamber in a normal bladder. The posterior wall of the intermediate tubular portion and the adjacent inner portion of the posterior wall of each sac are continuously thickened by the development of a thick mass of vertically disposed fibres (fig. 40, *p.p.*). On the ventral surface of the hinder part of the complex centrum these fibres separate into two bundles which pass dorsally one on each side of the centrum, and ultimately after curving slightly forwards become firmly inserted by their dorsal edges into the lateral surfaces of the complex centrum, and into the posterior margins of the dorsal laminæ (fig. 39, *d.l.*). It is evident that these skeletally attached fibres almost precisely resemble the posterior pillars of a normal anterior chamber. In addition, the anterior wall of each air-sac is attached to the anterior margin of the modified transverse process by a superficial stratum of fibres which separates from the rest of the wall and is inserted into the process in question. More internally the same stratum is attached to the lateral surface of the complex centrum and to the corresponding dorsal lamina. The crescentic process of each tripus (fig. 40, *tr.c.*) is imbedded in the dorsal wall of the contiguous air-sac, near the antero-internal angle of the latter. The relations of the process to the principal sheets of fibres in the dorsal wall appear to be perfectly normal. Thus, the fibres constituting the inner stratum of the mesial part of the anterior wall have the usual insertion into the radial nodule and ventral surface of the tripus, but from this point outwards the fibres forming the inner stratum, as well as those of both the inner and outer strata of the lateral wall, and the outer portion of the posterior wall of each sac, extend into the dorsal wall and finally converge to their insertion into the convexity of the crescentic process (fig. 40). It will be obvious, therefore, that but for the insertion of the fibres of the inner stratum of the tunica externa of the lateral and dorsal walls of each air-sac directly into the tripus the skeletal attachments of the anterior and lateral walls are almost precisely the same as in the anterior chamber of *Platystoma* and other Pimelodinæ with normal bladders.

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* In a specimen three inches long the antero-posterior extent of each sac was 3·5 mm., and the transverse 4 mm.

The most interesting feature in connection with the air-bladder of this species is, that while its small size and partial constriction into two lateral air-sacs would suggest that it represents an incipient stage in the kind of retrogressive modification of which *Bagarius* and *Glyptosternum* are extreme examples, it nevertheless retains its normal attachments both to rigid portions of the skeleton and to the tripodes, as well as the structural integrity of its walls, and the usual connection with the alimentary canal.

The ventral surfaces of the two air-sacs are invested by an unusually large mesonephros, which also extends laterally and, in conjunction with the peritoneal hepatic pouches and their contents, separates each sac from the adjacent lateral cutaneous area. The mesonephros of the right side only accompanies the corresponding posterior cardinal vein to join its anterior lymphoid portion. The latter part of the gland occupies on each side a recess between the inferior limb of the post-temporal and the transverse process of the fourth vertebra, and is in contact dorsally with the floor of the saccus paravertebralis and continuous with its fellow by a slender connecting lobe which crosses the ventral surface of the body of the first vertebra.

A fairly stout ligament stretches transversely between the recurved distal extremities of the modified transverse processes, in contact with the proper anterior walls of the two air-sacs, but is firmly attached in the median line to the body of the first vertebra.

Neither compressor nor tensor tripodis muscles are present in this species.

The Weberian ossicles differ but little from those of the more normal species of Pimelodinæ. The crescentic process of the tripus (fig. 41, *tr.c.*), however, has but a slight inward curvature. Claustra are present.

Pimelodus sapo.

Both in the structure of its air-bladder and in the modifications of the anterior vertebræ and their processes this species presents a singular and somewhat unexpected contrast to the more normally constituted species of the genus.

The complex, the fifth, and the sixth vertebræ are rigidly connected together by the growth of superficial ossifications and the partial anchylosis of their neural arches and spines. The centrum of the first vertebra (fig. 37, v^1) is a comparatively thin, biconcave disc, firmly united to the anterior end of the complex centrum. The complex and fifth centra are about equal in size, and each is but a little longer than the centrum of the sixth vertebra (*c.c.*, v^5, and v^6). Superficial bony deposit has considerably thickened the lateral surfaces of the complex and fifth centra, and, to a slight extent, the centrum of the sixth vertebra also, so that these centra appear much wider as well as shorter than the corresponding elements in the more normal species of *Pimelodus.* By the ventral and lateral extension of this superficial ossification, the grooves for the dorsal aorta and posterior cardinal veins become converted into bony canals (*a.c.*, *cd.c.*). Immediately behind the anterior opening of the aortic canal, the ventral and lateral surfaces of the complex centrum are encircled by an obliquely disposed crescentic thickening, in the form of a ridge, which constitutes the anterior boundary of a deep but narrow groove, opening laterally on each side into the recess enclosed by the modified transverse processes of the fourth vertebra, and receiving the anterior margins of the mesial and inner lateral portions of the air-bladder. Small radial nodules are suturally attached to the lateral surfaces of the complex centrum, and each nodule is in fibrous continuity with a slender spicular dorsal lamina having the usual relations to the anterior opening of the cardinal canal and to the transverse process of the fourth vertebra.

Not only is the transverse process of the fourth vertebra (*t.p.*^{4}) greatly expanded, but for the proximal third of its extent the anterior margin is bent downwards, and for the distal two-thirds not only downwards but also backwards towards the posterior margin. The posterior edge of the process is also decurved, but to a somewhat less extent than the former. By these modifications each process forms the outer walls of a flask-shaped recess which is open posteriorly and distally in the dry skeleton, but closed behind by a tough fibrous membrane, and at the distal extremity by the lateral cutaneous area of its side in the fresh specimen. The recess is slightly expanded distally, somewhat contracted towards the centre, and again expanded at the root of the process into a relatively spacious cavity for the reception of the inner lateral cæcal portion of the air-bladder. The decurved anterior margin of the process articulates by means of a facet on its anterior face with the inferior limb of the post-temporal (*pt.i.*), while the distal edge of its recurved portion forms part of the inner wall of the socket for the clavicle (*cl.s.*), the outer wall being formed by the greatly elongated post-temporal stem (*pt.s.*). The recurved portion also forms the lower lip of the distal opening of the enclosed recess. The transverse process of the fifth vertebra is much larger than any of the normal processes, and for the whole extent of its anterior margin is suturally united to the preceding process (*tp.*^{5}). The transverse process of the next vertebra (*tp.*^{6}), which is much shorter and thicker, is widely separated from the foregoing and carries the first rib (*r.*′).

As the result of its extremely degenerate condition the air-bladder is very curiously modified. It consists of a median portion (*a.b.*) which is flattened, leaf-like, and apparently solid, and of two lateral out-growths on each side. Of these out-growths the outer lateral one (*o.l.*) is also thin and solid, and, after curving forwards and inwards like a broad crescent, ultimately contracts rather abruptly into a slender tubular portion which bends upwards and inwards and ends blindly near the ventral wall of the saccus paravertebralis in the substance of the anterior lymphoid portion of mesonephros.* The inner lateral out-growth (*in.l.*), on the contrary, is a hollow and relatively spacious cæcum, with fairly thick walls, which, after leaving the median part of the bladder, curves round the lateral surface of the complex centrum in the oblique groove to which reference has already been made, and finally enters the deep bony recess on the ventral side of the root of the modified transverse process where it slightly expands and becomes connected by its dorsal and inner walls with the tripus and the radial nodule respectively. No portion of the air-bladder extends into the distal two-thirds of either recess. At its blind anterior extremity the walls of the inner lateral cæcum are much thinner than elsewhere, but its cavity is practically distinct from that of its fellow of the opposite side. With the exceptions above mentioned, the whole of the air-bladder is apparently solid although denser externally than internally. The solidity of the organ is, however, really due to the almost complete obliteration of its original cavity by the development of a dense internal reticulum of anastomosing fibrous bundles. The median portion of the bladder, and especially the anterior part of it, is closely adherent to the ventral and lateral surfaces of the complex centrum. We could discover no trace of a ductus pneumaticus unless a slender solid fibrous cord extending from the flattened median part of the bladder to the dorsal wall of the œsophagus may be regarded as a vestige of it.

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* It is possible that the outer lateral cæcum is a degenerate remnant of the antero-lateral cæca of other Siluridæ (*e.g.*, *Platystoma*).

The mesonephros accompanies the right posterior cardinal vein through the cardinal canal, and at the anterior extremity of the latter expands into its usual lymphoid portion. The latter part of the gland surrounds the anterior extremity of the inner lateral cæcum, and also the tubular portion of the outer lateral diverticulum, and, in addition, extends into the contracted median part of each flask-shaped recess.

Except for its relatively small size the tripus is fairly normal (fig. 38, *tr.*). Compared with the anterior process (*tr.a.*) the crescentic section of the ossicle (*tr.c.*) is rather short, with a sharp hooked curvature. The articular process (*tr.ar.*) tapers to a point at its distal extremity. The crescentic process is imbedded in the dorsal wall of the anterior extremity of the inner lateral cæcum. The convergence of the fibres of the inner stratum of the tunica externa to their insertion into the convexity of the crescentic process is very obvious, as also is the attachment of the concavity of the same process to the radial nodule by means of radial fibres, but the disposition of the usual curvilinear fibres of the outer stratum is not so easily traceable, although there is no doubt as to their insertion into the tripus. The intercalarium is a very small bony nodule in the interossicular ligament. Except that it has no ascending process the scaphium is normal. The claustra are slender spicular ossicles in the usual position.

It need scarcely be added that there is no trace of compressor or tensor tripodis muscles.

The cavum sinus imparis and the atrial cavities are normal, but we could not with certainty satisfy ourselves as to the presence or absence of a sinus endolymphaticus.

Callophysus macropterus.

Under the name of *Pimelodus macropterus*, JOHANNES MÜLLER (28, Plate 4, fig. 7) figures and briefly describes the air-bladder of this species. The organ is said to be small, heart-shaped, and flat, and to be surrounded along its sides and at the hinder end by an elegant wreath of small blindly ending diverticula. Anteriorly, where in *Platystoma fasciatum* a single pair of cæcal appendages is present, MÜLLER found, on each side a very long, wide, blind diverticulum.

Auchenoglanis biscutatus.

With one exception (*Pimelodus platychir*), *Auchenoglanis* is the only African representative of the essentially South American group of Pimelodina, and, in so far as its air-bladder and skeleton are concerned, has but little in common with the other normal members of the group.

As regards the modifications of the anterior vertebræ and their processes, *Auchenoglanis* somewhat closely resembles *Pseudobagrus* or *Rita.* The first eight vertebræ are rigidly connected together, the ninth being the first of the flexibly articulated series. The body of the first vertebra is a thin slightly biconcave discoidal bone. The anterior face of the complex centrum (fig. 42, *c.c.*) is also discoidal with a relatively shallow concavity, but for the rest of its extent the centrum is laterally compressed, its posterior concavity being deep and almost tubular. The complex centrum is about half as long again as the centrum of the fifth vertebra. The latter ($v.^{5}$) is similarly unsymmetrical in the relative depths of its concave surfaces, and nearly twice the length of any of the succeeding centra. Instead of the arch of the complex vertebra forming, as it almost invariably does, a continuous lamina of bone on each side of the neural canal, its anterior third is separated from the posterior two-thirds by a well-marked irregularly shaped cleft, which not only indicates the distinctness of the usually confluent arches of the third and fourth vertebræ, but also extends dorsalwards and is evident as a suture separating the large spinous process of the third from the rudimentary spine of the fourth vertebra.

A continuous deposit of superficial bone thickens the lateral surfaces of the compressed centra of the complex and fifth vertebræ, and is also continued posteriorly in the form of stout ventro-lateral ridges as far as the seventh centrum. There is a deep median aortic groove on the ventral surfaces of these centra bounded by prominent lateral ridges. The posterior cardinal vein traverses, not a canal, but a deep groove (fig. 42, *cd.g.*) on the sides of the complex and fifth centra, between the dorsal edge of the superficial ossification and the roots of the adjacent transverse processes, and only for a short distance in the region of the dorsal lamina (*d.l.*) does the vein become completely surrounded by bone. The ventral margin of the anterior face of the complex centrum is produced downwards and laterally into a somewhat fan-shaped, transversely disposed, plate of bone (*sv.p.*) which is cleft in the median line for the passage of the dorsal aorta. Two similar but smaller processes ($sv.p.^{1}$) are developed from the corresponding margin of the body of the first vertebra and become suturally applied to, without anchylosing with, the former pair. These paired bony outgrowths may, in part, represent the accessory articular processes of the complex and fifth vertebræ, but if this be so, there can be little doubt that they have been greatly strengthened by the extension of the superficial ossifications from the complex centrum into the mesial portion of the outer stratum of the tunica externa of the anterior wall of the air-bladder.

The anterior division of the transverse process of the fourth vertebra ($t.p.^{4}a.$) is very stout, slightly decurved, and flattened antero-posteriorly towards its distal extremity, where it is applied to the expanded outer extremity of the inferior limb of the post-temporal. The posterior division is broad and flat ($t.p.^{4}p.$), continuous for the most part with the anterior division, but separated therefrom at its distal extremity by a wide cleft. The transverse process of the fifth vertebra ($t.p.^{5}$) is both longer and broader than any that follow, and partially confluent at its root with the preceding process. The transverse processes of the sixth vertebra carry the first pair of ribs and are quite free.

The radial nodule (*r.n.*) is a somewhat elongated ossification, loosely attached by fibrous tissue to the lateral surface of the complex centrum, and by the same means connected also with the slender dorsal lamina (*d.l.*), which, after passing beneath the posterior cardinal vein blends with the ventral surface of the transverse process of the fourth vertebra.

The air-bladder (fig. 44) has no extrinsic muscles comparable to the compressor and tensor tripodis muscles of the South American *Pimelodinæ.* Its walls are fairly thick, and its lateral compartments devoid of any trace of secondary transverse septa. The primary transverse septum (*t.s.*) stretches completely across the bladder, but two large circular apertures place the anterior and lateral compartments in free communication with one another. The skeletal attachments of the anterior wall are similar to those of *Platystoma,* except that the median portion of its outer stratum is firmly attached to and supported by the fan-shaped sub-vertebral processes. The attachments of the converging fibres of the antero-lateral, lateral, and dorsal walls of the anterior chamber to the tripodes are normal. Fig. 44 shows the outer stratum of the tunica externa of the anterior wall (*o.st.*), and incidentally also, the lateral peritoneal cul-de-sacs (*p.c.s.*), in which the small lateral lobes of the liver are lodged, the recesses which contained the anterior lymphoid lobes of the mesonephros (*mph.r.*), and the aponeurotic membrane bounding these recesses anteriorly and dorsally (*ap.m.*).

The Weberian ossicles require no special description. The anterior process of the tripus (fig. 43, *tr.a.*) is very broad in proportion to its length, and has its anterior extremity greatly thickened for the attachment of the stout interossicular ligament. The crescentic process (figs. 43, 44, *tr.c.*) is rather stout, with a relatively slight and somewhat open curvature, and a decurved inner extremity. The intercalarium is a stout nodule in the interossicular ligament. The scaphium has a comparatively small spatulate process.

The more noteworthy features in which *Auchenoglanis* differs from the majority of other normal *Pimelodinæ* are (*a*) the restricted extent of the superficial ossifications, which consequently fail to extend laterally on to the modified transverse processes, or ventrally round the dorsal aorta, so that the channels both for the dorsal aorta and the posterior cardinal veins remain as open grooves, instead of complete bony canals; (*b*) the presence of paired sub-vertebral processes for the support and attachment of the anterior wall of the bladder; (*c*) the absence of lateral cæcal outgrowths, of secondary transverse septa, and of compressor or tensor tripodis muscles.

GROUP—ARIINA.

Arius pidada.

As the genus *Arius*, of all the genera of Siluroid Fishes the most cosmopolitan in its geographical distribution, not only includes a considerable number of species, but is also fairly typical of several other genera in so far as the modifications of the anterior vertebræ and the structure of the air-bladder are concerned, we venture to give a detailed account of these structures in the Javan species, *Arius pidada.*

The series of rigidly interconnected anterior vertebræ includes the first, the complex, and the fifth, sixth, and seventh vertebræ, all of which are also firmly connected with the skull, partly by reason of the anchylosis of the accessory articular processes of the basioccipital and complex centrum, and partly by the extension of a pair of bony laminæ between the supraoccipital and the modified transverse processes of the fourth vertebra.

Relatively to the normal centra the body of the first vertebra is very small, and though visible in the floor of the neural canal, of which its dorsal surface forms a part, is hidden ventrally by the coalescence of the accessory articular processes of the basioccipital and complex centrum; laterally, it is to a slight extent visible on the exterior, wedged in between the complex centrum and the base of the skull (figs. 45 and 46, *v.*^{1}). The complex centrum is much elongated and has its posterior concavity deeper than the anterior (fig. 46, *c.c.*). Two pairs of nutrient foramina are visible on its ventral surface, in the roof of the aortic canal, which belong to the third and fourth vertebræ respectively (fig. 46). The body of the fifth vertebra (*v.*^{5}) is smaller than the complex centrum which, however, it resembles in having the posterior concavity much deeper than the anterior. The sixth centrum is somewhat larger than the seventh but both are normal, except that their lateral surfaces are invested by the superficial ossifications (*v.*^{6}, *v.*^{7}). The eighth vertebra is normal and free (figs. 45 to 47, *v.*^{8}).

The neural arches of all the anterior vertebræ from the complex to the seventh inclusive, are partially anchylosed together, only faint indications of sutures being observable between them (fig. 46).

The neural spines of the third and fourth vertebræ are long and stout; the former is inclined forwards over the neural canal in the region of the first vertebra, and abuts against the supraoccipital and exoccipitals, but a small amount of intercalated cartilage still persists in a cleft in its anterior margin (fig. 46, *n.s.*^{3}); the latter, on the contrary, is directed obliquely backwards and cleft at its distal extremity, and grooved along its posterior margin for the support of the two large anterior interspinous bones of the dorsal fin (*n.s.*^{4}). The spines of the four succeeding vertebræ are obsolete. The ninth vertebra has a pair of rudimentary spines and the tenth and following vertebræ large spines, which are bifid in the region of the dorsal fin (fig. 46).

A very characteristic feature in *Arius pidada*, and in all the Arioid genera and species that came under our notice, is the existence of a stout conical subvertebral process of bone which grows downwards from the ventral surfaces of the anterior portion of the complex centrum, the body of the first vertebra, and the hinder part of the basioccipital (figs. 45 to 48, *sv.p.*). All three bones apparently take part in its formation, but the basioccipital to a much greater extent than the others. The process is broad at its origin, somewhat laterally compressed for the greater part of its extent, but flattened from before backwards at its free ventral extremity. Its base is perforated by the commencement of the aortic canal. The subvertebral process is closely applied to the mesial portion of the anterior wall of the air-bladder, but, except at its distal extremity, there is no fibrous connection between the two (fig. 48, *sv.p.*). The formation of the process seems to have been due to the enormous enlargement of the accessory articular processes of the basioccipital and the centra of the first and complex vertebræ (see *Macrones*, p. 76, figs. 4 and 5), but if this be so their original paired arrangement is now completely obscured by ventral coalescence beneath the dorsal aorta. There can, however, be little doubt that the superficial ossifications by their extension into the median portion of the transverse membrane, and possibly also into that part of the aponeurotic membrane which invests the ventral surface of the basioccipital, combined with their subsequent fusion with the processes in question, have largely contributed to the growth of the subvertebral process. A somewhat intermediate condition between the ordinary accessory articular processes of *Macrones* and the subvertebral process of *Arius* and its allies is to be found in *Auchenoglanis* and one or two other genera, where the articular processes retain their usual paired arrangement, but those belonging to the complex centrum, and to a lesser extent those of the first vertebra also, obviously owe their lateral growth to an extension of bony deposit from the superficial ossifications into the outer layer of the tunica externa of the anterior wall of the air-bladder.

As in *Platystoma*, the superficial ossifications are very strongly developed (figs. 45 and 47, *so.s.*). Not only do they continuously invest the lateral surfaces of the anterior vertebræ from the complex to the seventh, inclusive, but, by their extension downwards and subsequent fusion in the medio-ventral line, they convert what is ordinarily a groove for the dorsal aorta into a complete aortic canal (figs. 46 and 47, *a.c.*). Laterally, the ossifications extend outwards from the sides of the centra and extensively invest the ventral surfaces of the transverse processes of the fourth and fifth vertebræ, and, in addition, slightly overlap the roots of the corresponding processes of the sixth and seventh vertebræ (fig. 47, *so.s.*). Anteriorly, the ossifications extends downwards towards the median line, and would seem to blend with the posterior face of the subvertebral process. At the posterior aperture of the aortic canal the confluent ossifications are deeply emarginate in the mid-ventral line. The shape of each ossification as it extends outwards from the vertebral centra to blend with the transverse processes is somewhat triangular, with the apex directed outwards and confluent with the transverse process of the fourth vertebra (fig. 47). The oblique anterior and posterior margins of the ossifications are nearly straight, but the posterior is much the longer of the two. As in *Platystoma*, the lateral extension of the ossifications from the sides of the vertebral centra on to the contiguous transverse processes converts the cardinal grooves into complete canals, the length of which nearly coincides with that of the series of modified and rigidly articulated vertebræ, but unlike *Platystoma*, the ossifications are not traversed by wavy or other lines indicative of intervertebral sutures.

A stout radial nodule is firmly attached to each of the lateral surfaces of the complex centrum near its anterior extremity, and at the base of the subvertebral process (fig. 47, *r.n.*). A faint oblique lateral ridge traverses each of the antero-lateral margins of the subvertebral process but scarcely reaches the radial nodule. The dorsal lamina (fig. 47, *d.l.*) is represented by a thin slender process of bone, which is prolonged from the radial nodule obliquely backwards and upwards, ventrad to the posterior cardinal vein, and finally blends with the ventral surface of the transverse process of the fourth vertebra. The posterior margin of the lamina is suturally joined to the anterior margin of the superficial ossification of the same side, and, consequently, to a slight extent, lengthens the corresponding cardinal canal.

The presence of transverse processes in connection with the centrum of the first vertebra is very exceptional in the Siluridæ. Ramsay Wright (42), however, has described a pair of very rudimentary processes in *Amiurus catus*, and a pair of short spicular outgrowths from the first vertebra in *Arius pidada* may possibly have a like significance, but that they correspond to those carried by the succeeding vertebræ is, to say the least, very doubtful. The transverse processes of the fourth vertebra are greatly developed. Each is somewhat fan-shaped, with a flattened and contracted root, and an expanded distal portion (figs. 45 and 47, $t.p.^4$). The anterior portion, representing the anterior division of the process ($t.p.^4a.$), is slightly thickened and strongly decurved, and, moreover, is produced distally into a pointed process which is applied to the cleft stem of the post-temporal so as to form, completely or partially, the posterior boundary of the socket for the clavicle. The posterior portion of the transverse process, which is much thickened, inclines obliquely backwards as well as outwards, and represents the usual posterior division of the process ($t.p.^4p.$). An extremely thin, curved, and apparently somewhat flexible lamina of bone extends between and connects the thickened anterior and posterior divisions. The relative thinness of this lamina, combined with the existence of a deep notch between the decurved anterior division and the complex centrum for the reception of the posterior section of the tripus, renders the anterior division slightly flexible and apparently capable of a limited amount of motion in an upward and forward direction. The transverse process of the fifth vertebra ($t.p.^5$) is much smaller but longer and more expanded than any that follow. Its distal extremity is free, but for the greater part of its extent the anterior margin of the process is suturally united to the posterior edge of the preceding process. The transverse process of the sixth vertebra (*t.p.*^{6}) is long and slender, free distally, but slightly overlapped proximally by the posterior edge of its predecessor. Its distal extremity carries the first rib (*r.*^{1}).

The expanded and otherwise modified transverse processes of the fourth, fifth, and sixth vertebræ, together with the superficial ossifications, form on each side a smooth, bony surface, concave from before backwards, and closely moulded to the convexity of the anterior and dorsal walls of the anterior compartment of the air-bladder. The strong development of the superficial ossifications and their median and ventral coalescence to form an aortic canal renders the subvertebral keel unusually prominent, and its groove-like impression in the medio-dorsal line of the anterior chamber exceptionally deep.

Except for the large size of the accessory articular processes of the basioccipital and their union with those of the complex centrum to form the subvertebral process, the structure of the hinder part of the skull substantially agrees with that of *Macrones.* The cranial recesses for the utriculi are unusually spacious, and are visible externally as prominent rounded bullæ on the surfaces of the auditory capsules near the postero-lateral angles of the skull. The cavum sinus imparis (fig. 46, *c.s.i.*) contracts towards its hinder extremity and communicates with the two atria by a comparatively small aperture. The posterior edge of its roof is produced downwards into a median process, which nearly meets the slightly upturned posterior margin of the basioccipital and strengthens the otherwise fibrous roof and posterior wall of the atrial cavities. The posterior face of the skull is firmly united to the anterior vertebræ by two broad shelving plates of bone which extend downwards from the lateral portions of the supraoccipital and suturally articulate with stout ridges on the dorsal surfaces of the transverse processes of the fourth vertebra (figs. 45, 46, *so.*^{2}). The supraoccipital spine (*so.*^{1}) is very strongly developed and extends backwards over the interspace between the divergent spines of the third and fourth vertebræ to its sutural union with the first interspinous bone or nuchal plate (*i.s.*). A thin lamina of bone is given off from the posterior plate of the exoccipital between the two foramina for the passage of the pneumogastric and hypoglossal nerves, and extends backwards towards the root of the first of the modified transverse processes; this plate forms the outer wall of a recess in which the saccus paravertebralis is lodged, the inner wall being formed by the adjacent lateral surfaces of the first vertebral centrum and the anterior portion of the complex centrum (fig. 47).

It will be observed that the union of the skull with the anterior vertebræ is unusually intimate in *Arius.* Apart from the partial anchylosis of the accessory articular processes of the basioccipital and complex centrum in the formation of the characteristic subvertebral process, the union of the paired supraoccipital laminæ and the median supraoccipital spine with the transverse processes of the fourth vertebra and the expanded first interspinous bone, respectively, renders the connection between the two structures exceptionally rigid.

The post-temporal is normal in shape, and in its relations to the skull and to the transverse processes of the fourth vertebra. The inferior limb of the bone articulates with a stout projection from the lateral surface of the basioccipital (fig. 47, *pt.i.*). The cleft in the stem of the post-temporal to form the clavicular socket is unusually deep (*cl.s.*). There are no post-temporal plates.

The air-bladder has the usual cordate shape, but its walls are exceptionally stout and rigid (fig. 48). Its anterior wall is traversed by a deep median vertical groove, due to the impression of the subvertebral process (*sv.p.*). As in most other normal Siluridæ, the cavity of the bladder is subdivided into an anterior (*a.c.*) and two lateral chambers (*l.c.*) by the usual ⅄-shaped disposition of the primary transverse (*t.s.*) and longitudinal (*l.s.*) septa; and the cavity of each lateral compartment is further subdivided by several secondary transverse septa (*t.s.'*). Strong buttresses of fibres pass from both faces of the secondary septa, and also from the posterior face of the principal transverse septum, and extend into the adjacent portions of the ventral wall of the two lateral compartments. The primary transverse septum (*t.s.*) is very thick, and inclines obliquely downwards and forwards from its dorsal attachment to the skeleton to its junction with the ventral wall of the bladder. Here, as in *Platystoma*, the obliquity of the septum has the effect of causing the lateral compartments to extend forwards for some little distance beneath the anterior chamber. The dorsal margin of the septum is firmly attached to the posterior and lateral edges of the superficial ossifications where the latter invest the body of the fifth vertebra, and, externally to this, to the ventral surfaces of the transverse processes of the same vertebra. The mesial portion of the anterior face of the septum is thickened into two stout, forwardly projecting, parallel ridges, which are continued dorsally to the skeletal attachments of the septum; ventrally the ridges extend downwards, and, at the same time, curve forwards along the inner surface of the ventral wall of the anterior chamber, while still retaining their parallel relations (*r.s.*)*; from the ventral wall the two ridges again extend dorsalwards on the posterior face of the anterior wall, where the fibres of which they are composed, with the addition of the remaining fibres of the median portion of the anterior wall, diverge in the form of two bundles (anterior pillars), and pass, one on each side of the complex centrum, to the lateral surfaces of which and to the radial nodules they eventually become attached. In the anterior wall the vertically disposed ridges are evidently the result of a special concentration of the vertical fibres, which normally, as in *Macrones*, form the inner stratum of the tunica externa in that region, while the parallel ridges of the ventral wall as clearly owe their existence to an excessive thickening of the inner stratum of longitudinal fibres, which continuously extends between the anterior wall and the primary transverse septum and their respective attachments to the skeleton. The special development of these fibres, and their concentration into strong inwardly projecting ridges, is probably to be correlated with the greater thickness of the walls of the anterior chamber in *Arius*. Functionally, the ridges may be compared to a more or less rigid skeletal structure, arch-like in shape, and with the convexity of the arch directed towards the ventral surface, thus rendering the anterior, posterior, and ventral walls of the anterior chamber rigid and unyielding, and therefore necessarily causing any increase or diminution in the internal capacity of the chamber to depend mainly, and probably solely, on the movements of its lateral walls. The projection of these ridges into the cavity of the chamber, combined with the strong median ridge which the impression of the subvertebral keel gives rise to in the dorsal wall, has the effect of reducing the communication between the lateral halves of the chamber to a relatively small oval foramen. (See *Ketengus typus*, fig. 50.) The walls of the compartment are perfectly smooth internally, and, laterally, are in contact with the cutaneous areas (fig. 48, *l.c.a.*).

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* In fig. 48 only the lateral portions of the ventral wall of the anterior chamber have been removed, the median portion remaining intact, except that an oval window has been cut in it in order to show the parallel ridges on its inner surface. The same figure also shows the obliquity of the primary transverse septum, and the forward extension of the two lateral compartments.

In the arrangement and skeletal attachments of the fibrous sheets forming the walls of the anterior chamber, *Arius* exhibits several features in which it differs from *Macrones*, and many other normal Siluroids that we have so far described. In the proper anterior wall the fibres forming the median portions of both the inner and outer strata of the tunica externa are closely coherent, and on the ventral surface of the anterior end of the complex centrum split into two diverging bundles, which pass dorsally, one on each side of the median line, and at their dorsal margins have the usual insertions into the lateral surfaces of the centrum, the radial nodules, and the ventral ridges on the crescentic processes of the tripodes. (See *Batrachocephalus mino*, fig. 52, *a.p.*) Externally to these skeletal attachments, on either side, the two strata become more easily separable, although still connected by scattered fibres passing from one to the other, but the fibres of the outer stratum, instead of extending into the dorsal wall and becoming attached to the tripodes, are inserted by their dorsal edges into the whole extent of the decurved anterior margins of the transverse processes of the fourth vertebra, including the distal extremities of the two processes, the insertion being posterior to the dorsal attachment of the transverse membrane (fig. 52, *t.p.*^{4}*a.*, *o.st.*). Traced from the anterior wall into either lateral wall the fibres of the outer stratum acquire the characteristic curvilinear disposition, and, if traced thence into the dorsal wall, converge in the form of thick triangular sheets to their ultimate insertion into the crescentic processes of the tripodes (*o.st.'*). The fibres forming the inner stratum of the tunica externa of the anterior wall on either side of the median skeletally attached portion have the normal vertical disposition, but become longitudinal, or slightly oblique, if traced thence into the dorsal wall, where they cross at right angles the converging fibres of the outer stratum to the outer side of each tripus, with which, however, they are in no way directly connected (fig. 48, *in.st.*). Traced from the anterior into the antero-lateral and lateral walls the fibres of the same stratum are still vertical, but in the dorsal wall become transverse, or at all events oblique, and nearly, if not quite, coincident in direction with the fibres of the outer stratum; nevertheless, none of these fibres appear to reach the tripodes, or become directly attached thereto, but thin away before reaching the crescentic processes of those ossicles. The inner stratum is relatively thin, and hence the triangular sheets which form the greater part of the dorsal wall of the anterior chamber are mainly composed of the converging fibres of the outer stratum. We have already pointed out that the subvertebral process is so closely applied to the anterior wall of the bladder as to produce in it a deep median groove, and we may add that the distal extremity of the process is attached thereto by fibrous tissue.

From a comparison of *Arius* and *Macrones* it will be obvious that the extent to which the anterior wall of the air-bladder is attached to the axial skeleton varies greatly in different Siluroids. In most of the genera with normal air-bladders that we have so far described, as for example in *Macrones*, the whole thickness of the mesial portion of the wall is attached dorsally to the lateral surfaces of the complex centrum, to the radial nodules, and to the ventral ridges of the tripodes, but laterally to this point, on each side, the inner and outer strata of the tunica externa behave differently in different genera. In *Macrones* and its allies both strata are continued into the dorsal wall, and eventually become inserted into the anterior part of the convexity of the crescentic process of each tripus. In *Arius*, on the contrary, the outer stratum in this region becomes disassociated, as it were, both from the tripus and the inner stratum, and firmly inserted by its dorsal margin into the anterior edge of the transverse process of the fourth vertebra. Variations may also be noted in the extent to which the fibres of the interior chamber are inserted into the tripodes. Thus in *Macrones*, all the fibres of the inner stratum in the lateral portions of the anterior wall, as well as those of the same stratum in the lateral walls, are prolonged into the dorsal wall and eventually become inserted into the tripodes; but in *Arius* the corresponding fibres, although traceable into the dorsal wall, thin away and disappear as a definite stratum without reaching or becoming directly attached to these ossicles. Hence it is that in the latter genus, the only fibres directly inserted into the tripodes are those which form the outer stratum of the tunica externa of the lateral walls and are subsequently prolonged into the dorsal wall in the form of stout triangular sheets, whereas in the former genus the fibres of both strata in the anterior as well as in the lateral walls, with the exception of the skeletally attached mesial part of the anterior wall, converge in the dorsal wall to the tripodes and are directly attached thereto. With reference to these variations it may be pointed out that *Platystoma* and other normal Pimelodinæ more closely approach the Arioid than the Macrones type in the extent and nature of the skeletal attachments of the anterior wall of the air-bladder, but while agreeing with *Arius* in the insertion of the dorsal edge of the outer stratum of the tunica externa into the anterior margins of the modified transverse processes of the fourth vertebra, *Platystoma* differs from that genus in having the fibres of the inner stratum of the lateral portions of the anterior wall connected dorsally with the tripodes, even though, as in *Arius*, the fibres of the same stratum in the lateral walls fail to reach the ossicles in question; and, consequently, in this respect *Platystoma* occupies an intermediate position between *Arius* and *Macrones.*

The more extensive attachment of the anterior wall of the bladder to immoveable portions of the axial skeleton is evidently a further provision to counteract any tendency on its part to participate in the distension or contraction of the anterior chamber, and consequently helps to restrict any diminution or increase in the capacity of that compartment to movements of the lateral walls which alone can influence the Weberian ossicles.

Unlike *Platystoma* a transverse membrane can be readily recognized in *Arius* as a thin but tough and inextensible layer of transversely or obliquely arranged fibres divided into two lateral halves by the subvertebral process. Each half is attached by its inner edge to the lateral surface of the process, and dorsally to the corresponding radial nodule and dorsal lamina, and in addition to the whole extent of the ventral margin of the decurved anterior edge of the transverse process of the fourth vertebra, from its root to its pointed distal extremity. At the antero-lateral angles of the air-bladder the fibres of this membrane pass from the extremities of the transverse processes and blend with the adjacent portions of the ventral wall.

The existence in *Arius* of a transverse membrane distinct from that layer of the tunica externa of the proper anterior wall of the bladder, which is also dorsally attached to the anterior margins of the modified transverse processes, removes one difficulty as to the exact nature of these structures in some Siluridæ. In the case of *Platystoma fasciatum*, which, in this respect, agrees with the species dissected by us (*P. tigrinum*), that part of the anterior wall which is attached to the transverse processes is regarded by SÖRENSEN (37) as representing the greatly thickened inner stratum of the peritoneal coat ("la plèvre"), and is therefore the equivalent of that special portion of the superficial coat of the bladder hitherto referred to by us as the transverse membrane.* In *P. tigrinum*, and presumably in *P. fasciatum* also, there is no transverse membrane distinct from the apparent proper anterior wall, and therefore, so far as these species are concerned, it is possible that the skeletally-attached outer stratum of the latter may be the equivalent of SÖRENSEN's "la plèvre" and our transverse membrane. But in *Arius* a skeletally-attached outer stratum of the anterior wall and a transverse membrane coexist, and consequently the one can scarcely be an equivalent to the other in cases where either is absent. Hence to us it seems more reasonable to assume that the skeletally-attached stratum of the anterior wall has much the same value both in *Arius* and *Platystoma*, and in each case is wholly or partially a portion of the tunica externa; and further, that the transverse membrane as a separable and distinct structure is entirely wanting in *Platystoma*—a fact which may possibly be associated with the extensive insertion of the great compressor muscles into the walls of the bladder. We have elsewhere, in our description of *Macrones*, given reasons for believing that even the transverse membrane is merely a special portion of the superficial coat of the air-bladder, which, for physiological purposes, has acquired certain fixed skeletal attachments, and with a similar object it is readily conceivable that, in addition, even a stratum of fibres belonging to the tunica externa of the anterior wall may also acquire a similar connection with rigid portions of the axial skeleton, such, in fact, as we have shown to be the case in *Arius* and in *Platystoma*, and other normal Pimelodinæ.

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* See *Macrones nemurus*, p. 90.

On the whole the Weberian ossicles in *Arius pidada* are very similar to those of *Platystoma*. The anterior process of the tripus (fig. 49, *tr.a.*) is somewhat shorter and of greater width than in most other Siluroids. The crescentic process (*tr.c.*) is rather thicker than usual, apparently in accordance with the greater thickness of the stratum of fibres attached to it, but on the ventral surface of its root the thickening abruptly ceases, leaving at that point a slight ridge, which, like the ventral ridge in *Macrones*, receives the insertion of a slip of fibres derived from the median portion of the anterior wall of the bladder. The crescentic process has no heel-like projection as in *Macrones*, nor is its posterior margin deeply grooved as in *Platystoma*. Claustra are present in the form of elongated spicular ossicles, slightly curved at their inferior extremities, and situated one on each side of the foramen magnum in contact with the posterior margins of the exoccipitals.

The more important characteristics of the Arioid type as exemplified by *Arius pidada* may be summarized as follows:—

(*a.*) The exceptionally firm anchylosis of the skull with certain of the anterior vertebræ, through the fusion of the greatly developed accessory articular processes of the basioccipital and complex centrum to form a stout subvertebral process, and the sutural union of the transverse processes of the fourth vertebra with the supraoccipital by the extension of a pair of strong osseous laminæ between the two structures.

(*b.*) The more extensive development of the superficial ossifications and their ventral and lateral extension to form complete bony canals for the dorsal aorta and the posterior cardinal veins.

(*c.*) The absence of post-temporal plates and the exclusion of the post-temporal bones from contact with the air-bladder, the modified transverse processes of the fourth vertebra, and the subvertebral process alone forming an effective bony support for its anterior wall.

(*d.*) The absence of compressor and tensor tripodis muscles, and of any tendency to the development of antero-lateral or other cæcal appendages in connection with the air-bladder.

(*e.*) The more extensive attachment of the lateral portions of the tunica externa of the anterior wall of the bladder to the skeleton by the separation of their thick outer strata from the inner, and the dorsal insertion of the former into the transverse processes of the fourth vertebra.

(*f.*) The existence of a distinct transverse membrane in addition to the skeletally attached outer stratum of the proper anterior wall of the bladder.

(*g.*) The concentration of the inner stratum of longitudinal fibres in the median portion of the ventral wall of the anterior chamber into two stout, inwardly projecting parallel ridges, and their extension into the anterior and posterior walls to the skeletal attachments of the anterior and posterior pillars respectively.

(*h.*) The failure of the fibres of the inner stratum of the tunica externa in the antero-lateral and lateral walls of the anterior chamber to reach their usual insertions into the crescentic processes of the tripodes.

(*i.*) The suppression of the ascending and horizontal processes of the intercalarium and the reduction of that ossicle to a small nodule of bone imbedded in the interossicular ligament.

It may be remarked that as regards the features indicated in paragraphs *b*, *c*, *e*, *h*, and *i*, *Arius* more or less closely resembles *Platystoma* and the other normal Pimelodinæ; but the distinctness of the Arioid type is, nevertheless, sufficiently emphasized by the facts referred to under *a*, *d*, and *f*.

In addition to *Arius pidada*, we have dissected the following Indian and Malayan species of the genus:—

A. sagor.
A. truncatus.
A. cœlatus.
A. venosus.
A. utik.
A. argyropleuron.
A. maculatus.
A. thalassinus.
A. arioides.
A. australis.

Of the African species, we have only been able to examine one example, viz., *Arius latiscutatus;* and of the South American representatives of this widely-distributed genus, a solitary example of *A. assimilis.*

All these species very closely resemble one another and *Arius pidada* in the structure of the air-bladder and the nature of the correlated skeletal modifications. Whatever variations do exist, appear to relate mainly to the relative thickness of the walls of the bladder, the greater or less number of the secondary transverse septa in the lateral compartments, or the relative size of the lateral chambers as compared with the anterior chamber. As a general rule, and as in most other normal Siluroids, the size of the air-bladder is approximately proportional to that of the Fish; and in cases where it is otherwise, any diminution in its capacity takes place at the expense of the lateral compartments; or, in other words, variations in the relative size of the anterior chamber in comparison with the bulk of the Fish are confined within narrower limits than is the case with corresponding variations in the size of the lateral chambers. The relation of such variations, and others of a similarly minor character, to particular species may be briefly noted.

In *Arius sagor* the subvertebral process is somewhat spatulate at its free distal extremity. The lateral walls of the anterior chamber are extremely thin over definitely circumscribed oval areas, which are in close relation externally with the lateral cutaneous areas.

In *Arius venosus* the walls of the bladder are not only very thick, but the component fibres of the tunica externa are so densely interlaced and matted together that their course can scarcely be traced beyond the triangular sheets of the dorsal wall of the anterior chamber.

In *Arius cœlatus,* and in one or two other species, the outer wall of each lateral chamber is strengthened internally by numerous vertically-disposed rib-like aggregations of fibres, separated by narrow intervening slits, and these may even extend forwards into the outer wall of the anterior chamber.

In *Arius australis* the air-bladder has particularly stout and rigid walls, and the obliquity of the primary transverse septum, especially of its mesial portion, is so great that its ventral edge extends nearly as far forwards as the anterior wall of the bladder before coalescing with the ventral wall; hence, the lateral compartments are prolonged as gradually contracting cavities on the ventral side of the inclined septum, nearly as far forwards as the anterior wall of the anterior chamber, but nevertheless remain separated from each other by a corresponding extension of the longitudinal septum. To a greater or less extent, this feature is characteristic of most species of *Arius*, but it is exceptionally well marked in this particular species.

In *Arius latiscutatus* there is but one secondary transverse septum in each lateral compartment.

Arius assimilis differs in no essential respect from its East Indian and African allies. The walls of the air-bladder, however, are extremely thin. Two short rudimentary secondary transverse septa are present in each lateral compartment.

In CUVIER and VALENCIENNES' great work (8) the air-bladder in several species of *Arius* is said to be provided with thick extrinsic muscles, as, for example, in *Arius cœlatus* and *A. milberti.* The latter species we have had no opportunity of dissecting, but certainly no such muscles are present in *A. cœlatus,* or in any other species of the genus that we examined.

If Dr. TAYLOR'S account (38) of the air-bladder of *Arius gagora* be correct, this species must possess a bladder of a very different type from any that we have met with in other species of the genus. According to this observer, there are two air-bladders, one on each side, enclosed in an osseous cup attached by a narrow stalk to the body of the "first" vertebra, close to its junction with the cranium. The mouth of each cup is said to be covered over by the common integument which, at this point, is extremely thin and adheres to the surface of the bladder, presenting, when the latter is distended with air, an "external elastic tumour" of an oval figure. The two air-bladders, which have no communication with each other, or with the alimentary canal, apparently derive their supply of air from a vascular tissue placed between the two cups where they are attached to the spine. The external coat is of a thin texture and argentine colour, and has a layer of fine adipose tissue interposed between it and the internal surface of the cup.

This description is so different from anything met with in other species of *Arius* that we are not at all surprised at DAY's statement (9, p. 708) that the air-bladder TAYLOR examined "could not have been in *Arius gagora*." From an examination of an example of this species taken at Mandalay, in Upper Burmah, DAY (*loc. cit.*) gives the following description of its air-bladder:—"Air-vessel large and somewhat heart-shaped, with a moderately thick external fibrous coat. On removing its front wall a longitudinal partition becomes apparent, but is not extended to its anterior portion. It has three transverse subdivisions forming it into five cavities, owing to the longitudinal partition commencing at the first transverse subdivision. These lateral cavities freely communicate with one another on the same side and with the opposite ones by means of the anterior chamber which does not possess any subdivision." From this account it is obvious that TAYLOR's description cannot apply to the air-bladder of a genuine *Arius gagora*, and, further, that this species possesses a perfectly normal bladder, subdivided internally by a primary transverse and a longitudinal septum, and, in addition, by two or more secondary transverse septa. It is not improbable that the species examined by TAYLOR was really *Callomystax gagata*; at any rate his description agrees fairly well with what we found in an example of the latter species.*

According to JOHANNES MÜLLER (28) the air-bladder of *Bagrus* (*Sciades*) *emphysetus* (MÜLL. and TROSCH.) (= *Arius emphysetus*, GÜNTHER) is very long, and consists of three bladders disposed in a longitudinal series, and communicating through their connecting constrictions.

Hemipimelodus borneensis.

In almost every respect the skeleton and air-bladder of this species closely conform to the Arioid type as illustrated by *Arius pidada*.

The walls of the air-bladder are very thick, but somewhat thinner in the antero-lateral and lateral regions of the anterior compartment than elsewhere. The primary transverse septum is also very stout, and its width such as to render the orifices whereby the lateral and anterior chambers intercommunicate comparatively small. Three stout secondary transverse septa are present in each of the two lateral chambers.

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* See p. 171.

DAY (9) briefly refers to the air-bladder in what he then regarded as examples of two Indian species of this genus, viz., *H. cenia*, HAM. BUCH., and *H. viridescens*, HAM. BUCH., in the following terms:—"The air-vessel is placed transversely across the body of the anterior vertebra. It has an expanded globular portion on either side enclosed in a bony capsule, and with a transverse connecting tube." This account is so greatly at variance with what we found in *H. borneensis* that we were not surprised to learn that DAY ('Proc. Zool. Soc.,' 1876, p. 794) subsequently admitted that the specimens he examined were species of *Gagata* (= *Callomystax*).

Ketengus typus.

In this species also both the air-bladder and skeletal modifications are very similar to those of *Arius pidada.*

Owing to the prominence of the sub-vertebral keel, and the extent to which the parallel ridges from the anterior, ventral, and posterior walls project inwards, the communication between the lateral halves of the anterior chamber is reduced to a relatively small and somewhat triangular foramen. Three pairs of secondary transverse septa sub-divide the cavities of the two lateral compartments.

A lateral view of the air-bladder with the outer wall of the right side removed, showing the dorsal ridge formed by the impression of the subvertebral keel (*sv.k.*), the parallel ridges (*r.s.*), and the foramen by which the lateral halves of the anterior chamber communicate with each other, is represented in fig. 50. In the same figure the primary and secondary transverse septa are also seen extending between the dorsal and ventral walls of the bladder (*t.s.*, *t.s.'*). The lettering, *a.p.* and *p.p.* indicates the anterior and posterior pillars of the anterior chamber.

Ælurichthys longispinis.

This Mexican Siluroid also bears a strong resemblance to *Arius pidada.* The walls of the air-bladder, however, are much thicker, and the dorso-lateral regions of the lateral compartments are strengthened internally by numerous column-like aggregations of vertically arranged fibres, separated by narrow slits, which become less marked and finally disappear towards the anterior chamber.

Ælurichthys Gronovii.

Under the name of *Galeichthys Gronovii*, CUVIER and VALENCIENNES (8) briefly refer to the air-bladder of this species. The organ is said to be heart-shaped, broader in front than behind, emarginate anteriorly, and somewhat flattened.

These writers also describe the bladder as possessing certain extrinsic muscles. Two long, straight muscles are said to be connected with its *dorsal* surface, while its ventral surface may be compressed by the contraction of two oblique muscles. If CUVIER and VALENCIENNES are correct in their description, the two oblique muscles may possibly correspond to the large compressor muscles which we have already described in the genera *Platystoma*, *Pimelodus*, and *Piramutana*. We have had no opportunity of examining this particular species, but we may safely assert that no such muscles, either dorsal or ventral, are present in *Æ. longispinis*.

Batrachocephalus mino.

In no essential feature is there any difference between the air-bladder and skeleton of this species and those of *Arius pidada*.

Relatively to the size of the body the air-bladder is rather large, and this is noticeably the case with the anterior chamber, which is both long and deep. Its walls are comparatively thin, and anteriorly are in close and extensive contact with large lateral cutaneous areas. Three pairs of secondary transverse septa incompletely subdivide the cavities of the two lateral compartments.

The general structure of the organ is represented in fig. 52, including the disposition and skeletal attachments of the principal sheets of fibres in the walls of the anterior chamber. In the left half of the compartment the arrangement of the fibres of the inner stratum of the tunica externa (*in.st.*) may be seen; on the right side the inner stratum has been removed so as to show the characteristic attachment of the outer stratum of the anterior wall (*o.st.*) to the transverse process of the fourth vertebra ($t.p.^4a.$), and the curvilinear disposition of the fibres of the same stratum in the lateral wall, and also their convergence in the dorsal wall in the form of a triangular sheet (*o.st.′*) to their insertion into the crescentic process of the tripus.

Osteogeniosus Valenciennesii.

In most of its osteological details this species* is almost identical with *Arius pidada*.

The air-bladder (fig. 51) is conical in outline, with a broad anterior, and a somewhat oval posterior, extremity. The anterior wall is rendered deeply emarginate in the median line by the impression of the subvertebral process (*sv.p.*) to which it is somewhat firmly attached by fibrous tissue. Internally the bladder is subdivided into anterior (*a.c.*) and lateral compartments (*l.c.*) by the usual transverse (*t.s.*) and longitudinal (*l.s.*) septa. The transverse septum has the normal attachment to the skeleton along its contracted dorsal edge, but towards the ventral margin widens considerably, and laterally is directly continuous with the ventral wall of the bladder;

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* The only reference to the air-bladder of this Indian Siluroid that we are acquainted with, is by DAY (9). He says, "In a specimen from Moulmein, taken in the river, the air-vessel was large, heart-shaped, having an internal longitudinal septum, and not enclosed in bone."

mesially, however, the septum becomes inclined obliquely forwards, and at the same time gradually narrows so as to form a thick triangular band of fibres, which extends as far forwards as the middle of the ventral wall of the anterior chamber, and finally becomes continuous therewith at its apex, as well as along its converging lateral margins. The two lateral compartments are continued forwards to the inclined median portion of the septum as far as the middle of the floor of the anterior chamber, in the form of two gradually contracting cavities, but remain separated from each other by a corresponding extension of the longitudinal septum along the posterior face of the inclined septum. Hence, as in some species of *Arius*, the anterior chamber is partially overlapped on its ventral side by the anterior extremities of both lateral compartments. A single, but extremely stout, secondary transverse septum (*t.s.'*) incompletely subdivides the cavity of each lateral chamber.

The lateral and posterior margins of the bladder are curiously compressed, and form, as it were, a solid flattened rim with a crenulated outline, partially encircling the organ. With the exception of the anterior wall, the walls of the bladder are, perhaps, thicker than in any other normal Siluroid, and so densely are their component fibres interlaced and matted together, that it is only in the dorsal wall, and, to a slight extent in the lateral walls of the anterior chamber, from whence the fibres which are ultimately inserted into the tripodes are derived, that any definite arrangement of them can be made out. The outer walls of both the anterior and lateral compartments are also greatly thickened internally by the aggregation of the fibres composing the inner stratum of the tunica externa into stout, vertically-arranged bundles, separated from one another by intervening slit-like sacculi. By the formation of these bundles internally, and the compression of the peripheral margins of the bladder, the lateral walls attain a thickness of nearly 4·5 mm. The secondary transverse septa, and the posterior face of the primary transverse septum, are thickened at their dorsal and ventral margins into ramifying root-like bundles of fibres, which fray out into the dorsal and ventral walls of the bladder, and finally blend therewith.

Relatively to the size of the fish, the apparent size of the air-bladder, when seen externally, is not less than in the various species of *Arius*, but the actual capacity of the internal cavities, and especially of the lateral compartments, is really very much smaller. This is partly due to the extraordinary thickness of its walls, and to the stoutness of the different internal septa, but also in a great measure to the flattened condition of the entire organ.

The comparatively small anterior chamber has its antero-lateral angles prolonged outwards into two small cæcal diverticula, which curve inwards in front of, and in contact with, the adjacent portion of the anterior wall. Each cæcum (*al.c.*) is deeply sacculated along its anterior margin; but otherwise its cavity is simple and undivided, and freely communicates with that of the anterior chamber.

The skeletal relations and attachments of the walls of the anterior chamber, as well as the structure of the triangular sheets of the dorsal wall and their mode of connection with the crescentic processes of the tripodes, are substantially the same as in *Arius pidada* and its allies, and this resemblance extends also to the condition of the Weberian ossicles.

Lateral cutaneous areas (*l.c.a.*) are formed by the divergence of the dorso-lateral and ventro-lateral muscles of the trunk, but a considerable amount of fatty tissue separates them from actual contact with the adjacent lateral walls of the anterior chamber of the air-bladder.

Osteogeniosus macrocephalus and *O. militaris.*

These species require no special notice. In each case the air-bladder is almost identical in structure with that of the preceding species.

GROUP :—BAGARINA.

Bagarius Yarrellii.

In *Bagarius* we again meet with an example of the effects of degeneration in retrogressively modifying the structure of the air-bladder.

CUVIER and VALENCIENNES (8) denied the presence of an air-bladder in *Bagarius*, but as far back as 1831, TAYLOR (38) had previously affirmed its existence in the form of two small sacs having no communication with each other or with the alimentary canal; and so small that each sac in a Fish weighing ten pounds was not larger than an ordinary garden pea. By the same observer it was also stated that the two sacs were situated one on each side of the body in a deep groove or furrow formed by the consolidated transverse processes of the cervical vertebræ, at about an equal distance from the common integument and the vertebral column, and immediately behind the pectoral fin. TAYLOR'S account was subsequently confirmed by DAY (9) in the following terms:—"Air-vessel small, consisting of two rounded portions situated on either side of the bodies of the anterior vertebræ, and partially enclosed in bone."

In the structure of the air-bladder and the nature of the correlated skeletal modifications *Bagarius* bears a strong resemblance to *Akysis* and *Acrochordonichthys*, but more particularly perhaps to *Glyptosternum*, of which an account will subsequently be given.

Mainly owing to the massive growth of the superficial ossifications the centra of the complex and fifth vertebræ are firmly anchylosed to each other, and to the skull (fig. 53). The centrum of the first vertebra is not only very small, but so completely is it enclosed within the contiguous concavities of the basioccipital and complex centrum, that no external indications of its existence can be detected. The centrum of the complex vertebra (fig. 53, *c.c.*) is very long, and its deep and almost equal anterior and posterior concavities nearly meet in the centre of the bone. The fifth vertebral centrum ($v.^5$) is much smaller, and although somewhat larger than the normal centra that follow it, otherwise resembles it. The sixth vertebra ($v.^6$) is quite free.

The neural spines of the third and fourth vertebræ are confluent and together form a thin, high, compressed plate of bone which is not cleft or in any other way modified for the support of the interspinous bones of the dorsal fin. The spinous process of the fifth vertebra is quite distinct from the foregoing, and deeply cleft. The neural arches of the complex and fifth vertebræ are completely anchylosed together, but remain distinct from the arch of the sixth. Three nutrient foramina are visible on the ventral surface of the complex centrum, two of which form a pair, and belong to the third vertebra, while the other is posterior to the former and median in position, and may therefore be regarded as belonging to the fourth vertebra.

The transverse processes of the fourth vertebra are curiously modified, each being greatly expanded and having, except at its thick flat root, the anterior margin curved downwards and slightly backwards towards the posterior margin, which also curves slightly downwards to meet it ($t.p.^4$). In this way the transverse processes form on each side a spout-like protuberance from the side of the complex vertebra, enclosing a cavity or recess which has complete bony walls in front, behind, and above, but is widely open towards the ventral surface. The anterior wall of each recess abruptly ceases at the flat root of the transverse process, and between its free inner margin and the lateral surface of the complex centrum there is a deep cleft, through which the tripus passes from its connection with the scaphium anteriorly to the air-bladder posteriorly. At the distal extremity of the process the anterior margin curves backwards towards the posterior margin to a somewhat greater extent than elsewhere, and slightly narrows the distal opening of the enclosed recess. The recess itself is somewhat oval in shape, being more expanded in the centre than it is distally or proximally. The anterior and posterior walls are fairly thick, but the dorsal wall thins away over a sharply-defined concave oval area, and consequently becomes adapted to the convex dorsal wall of the contained air-sac. The anterior lip of the distal aperture of the recess is marked by a roughened concave surface, which becomes applied to the stem of the post-temporal in such a way as to form, in conjunction with the latter, an articular socket for the proximal extremity of the clavicle. The transverse process of the fifth vertebra ($t.p.^5$) is very strongly developed, with a pointed free distal extremity and an expanded root, the anterior margin of which is partially confluent with the decurved posterior margin of its spout-like predecessor; the process also helps to deepen posteriorly the recess in which each lateral air-sac is lodged. The two foramina visible on the ventral surface of the process transmit the rami ventrales of the fifth and sixth spinal nerves ($sp.n.^5$, $sp.n.^6$).

Without forming an aortic canal, or even more than the merest trace of a groove for the dorsal aorta, the superficial ossifications invest and considerably thicken the lateral surfaces of the complex and fifth vertebral centra, and, probably as the result of a further extension of ossification into the dorsal portion of the aponeurotic membrane, extend even on to the lateral and ventral surfaces of the basioccipital, completely obscuring all external indication of the body of the first vertebra, and at the same time leading to the complete anchylosis of the base of the skull with the anterior vertebral centra. Faint traces of the intervertebral sutures between the centra of the complex and fifth vertebræ, and between the former and the basioccipital, may, however, be seen on the ventral surface (fig. 53). On each of the lateral surfaces of the complex centrum the superficial ossification is thickened into two longitudinal and parallel ridges, one lying dorsad to the other with a groove between them. The ventral ridge coincides with the ventro-lateral margin of the centrum, and is shorter than the dorsal ridge. Opposite the root of the spout-like transverse process the ventral ridge is produced outwards into a slender, triangularly-shaped, ventral process, the pointed apex of which is inserted into a thin, but tough, fibrous membrane investing the ventral wall of the lateral air-sac of its side (*v.p.*). The dorsal ridge (*d.r.*) appears to commence as a prolongation of the anterior margin of the transverse process of the fifth vertebra, and from thence is continued somewhat obliquely inwards and forwards along the side of the complex centrum, immediately beneath the root of the modified transverse process and dorsad to the ventral ridge, as far as the basioccipital, where it finally dies away beneath the lower lip of the external atrial aperture. The groove between the two ridges, which is much better marked on the right than on the left side, probably transmits the posterior cardinal vein and the paired anterior lobes of the mesonephros. A third ridge is formed by a thin prolongation of the anterior margin of the root of the modified transverse process, along the lower border of the forwardly-inclined neural arch of the third vertebra, as far as the upper lip of the external atrial aperture. Where this ridge and the dorsal ridge overlap, the former is dorsad to the latter, and in a narrow slit-like groove between the two the anterior process of the tripus (*tr.a.*) passes forwards to its attachment to the scaphium anteriorly. The external atrial aperture is situated at the anterior extremity of this groove, and near its hinder end the groove deepens into a pit, at the bottom of which the articular process of the tripus articulates with the lateral surface of the anterior third of the complex centrum; posteriorly, the groove opens into the recess enclosed by the spout-like transverse process.

We were unable to identify with certainty the usual oblique ridges on the sides of the complex centrum, or dorsal laminæ, neither could we detect any radial nodules. It may not improbably be the case, however, that the well-marked ridge (dorsal ridge) which leaves the ventral surface of each of the transverse processes of the fifth vertebra, and extends obliquely forwards and inwards along the adjacent lateral surface of the complex centrum, may represent both the lateral ridge and dorsal lamina of other and more normal Siluridæ; but if this be so, it is somewhat surprising that these structures should be so well developed when the diminutive and rudimentary condition of the air-bladder is taken into consideration. It must be admitted, however, that our suggestion receives some support from the fact that in the allied genus *Glyptosternum*, where a definitely recognisable dorsal lamina is present, there is no trace of the dorsal ridge.

The post-temporal* has its ascending process and stem somewhat expanded, but the inferior limb (*pt.i.*) is an extremely slender process, which, after leaving the stem, is firmly applied if not actually anchylosed to the distal extremity of the transverse process of the fourth vertebra, but nevertheless becomes detached therefrom as it passes inwards, and eventually fuses with the anterior end of the dorsal ridge on the lateral surface of the basioccipital. The socket for the clavicle is in part formed by a deep groove in the post-temporal at the junction of the stem with the inferior limb, and in part by the distal extremity of the modified transverse process which converts the groove into a tubular socket.

The air-bladder is represented by two thin-walled oval sacs, which occupy the bony recesses formed by the spout-like transverse processes of the fourth vertebra (fig. 53, *a.s.*). In proportion to the bulk of the Fish the size of the air-bladder is extremely insignificant, and it is evident that beyond a certain period, which is probably reached at a very early stage, the bladder does not increase in size with the growth of its possessor. In our specimen a very immature Fish, of not more than 6 inches in length, and probably weighing less than 3 ounces even when fresh, each air-sac was about 4 mm. long and 3·5 mm. wide, that is to say, about the size of an ordinary garden pea, which, according to TAYLOR (38), was also the size of an air-sac in a specimen weighing 10 pounds. We could discover no trace of any communication between the two sacs, or of lateral compartments, or of the existence of a ductus pneumaticus. The ventral surface of each sac is invested by a thin but tough fibrous membrane, which stretches between and is firmly attached to the decurved anterior and posterior margins of the modified transverse process, and would seem also to extend from one sac to the other across the ventral surface of the complex centrum. The distal openings of the bony recesses are closed by their respective lateral cutaneous areas, but the outer wall of each air-sac is separated from the latter by a certain quantity of fatty tissue, as well as by a portion of the lateral lobe of the liver. As in other Siluridæ, the walls of the air-bladder are firmly attached to the contiguous skeletal elements at certain points. The posterior wall of each air-sac blends with the investing fibrous membrane, which we must identify as the ventral portion of the superficial coat of the air-bladder, and the two are dorsally attached to the anterior margin of the transverse process of the fifth vertebra, and also to the posterior portion of the dorsal ridge as the latter passes on to the side of the complex centrum, much in the same way that the lateral portions of the posterior wall (*i.e.*, the primary transverse septum) of a normal anterior chamber are inserted into the dorsal lamina

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* In fig. 53 only the inferior limb is represented, the remainder of the bone having been removed.

—a fact which supports our suggestion that this ridge is in part the equivalent of the dorsal lamina in other Siluridæ. In a precisely similar manner the anterior wall is firmly adherent to the decurved anterior margin of the transverse process of the fourth vertebra. The inner wall of the air-sac is also attached to the dorsal ridge, where the latter traverses the side of the complex centrum. The only other point at which each air-sac is attached to a rigid portion of the skeleton is about the centre of its ventral wall, where the latter blends with its investing superficial coat, and both become firmly attached to the triangular outgrowth from the ventral ridge.

The straight posterior process of the tripus lies near the inner extremity of each air-sac in relation with the imperfect dorsal wall of the latter, but we were only able to detect a few fine-scattered fibres extending from the outer margin of the process obliquely outwards and forwards towards the antero-lateral and anterior walls of the sac. These fibres appear to be all that represent the thick triangular sheet of fibres which is so characteristic of each half of the dorsal wall of a normally developed anterior chamber, and are practically confined to rather less than the anterior half of the dorsal wall of the sac. In the posterior half of the dorsal wall we could detect only a thin stratum of connective tissue, which probably belongs to the tunica interna, although we could not with certainty detect any epithelium on its inner surface. No radial fibres could be made out.

The tripus (fig. 54, *tr.*), is a simple triradiate ossicle, with a long anterior process (*tr. a.*), which is connected with the scaphium by a relatively short interossicular ligament, a tapering articular process (*tr. ar.*), and a posterior division (*tr. c.*) which remains in a straight line with the anterior process, and tapers to a point at its hinder extremity without describing the normal crescentic curvature. The scaphium has no ascending process, but its horizontal spatulate portion terminates posteriorly in a spherical condyle. The intercalarium is a very small nodule of bone imbedded in the interossicular ligament. Claustra seem to be entirely absent.

The cavum sinus imparis and the atrial cavities are extremely small, but otherwise normal. We had no difficulty in detecting a transverse ductus endolymphaticus, but a most careful examination failed to reveal any trace of a sinus endolymphaticus.

Glyptosternum platypogon.

Under the name of *Pimelodus platypogon*, Cuvier and Valenciennes (8) describe this Siluroid as being devoid of an air-bladder. In a paper published in the Linnean Society's 'Journal,' vol. 13, Day, in referring to *Glyptosternum telchitta* remarks, "I cannot detect any air-vessel in this species." In 1871 ('Proc. Zool. Soc. Lon.,' p. 289), Day corrected his previous statement, and in again referring to the same species tersely describes the air-bladder as consisting of "two rounded lateral portions, very thin, and entirely enclosed by bone." In a later paper in the same year ('Proc. Zool. Soc.,' 1871, p. 714), he again refers in equally brief terms to *Glyptosternum* as having "an air-vessel in two rounded lateral portions, and enclosed in bony capsules," but in neither instance does he give any precise or detailed account of the organ. Of the general accuracy of DAY's brief description there can be no doubt, inasmuch as *Glyptosternum* affords a further illustration of the type of rudimentary air-bladder to which we have already directed attention in our account of *Akysis*, *Acrochordonichthys*, and *Bagarius*, but as regards the extent to which the diminutive air-bladder is incapsuled by bone, his account does not accurately apply to *G. platypogon*, which is the particular species we have examined, and the one in which CUVIER and VALENCIENNES denied its existence.

Of the various abnormal genera that so far have come under our notice, *Glyptosternum* most nearly resembles *Bagarius* in the structure of the air-bladder, and the condition of the modified anterior vertebræ. The body of the first vertebra is, however, somewhat better developed, but, although clearly visible on the ventral surface, it is almost completely excluded from forming any portion of the floor of the neural canal by the apposition of the dorsal edge of the basioccipital and the corresponding margin of the complex centrum (fig. 55, *v.′*). The first, the complex, and the fifth vertebræ (*v.*^{1}, *c.c.*, and *v.*^{5}) are rigidly united to one another and with the skull, but the union is entirely due to the character of the persistent sutural articulation of the different cranial or vertebral elements and not to their anchylosis, or to the growth of continuous superficial ossifications. The intervertebral sutures between the centra are clearly seen on the ventral and lateral surfaces, as also is the suture between the neural arches of the complex and fifth vertebræ on the lateral aspect. The body of the complex vertebra (*c.c.*) is much larger than that of the fifth vertebra (*v.*^{5}), and in each case the anterior and posterior concavities are about equal in depth. The sixth vertebra (*v.*^{6}) is quite free, being movably articulated with the foregoing.

The confluent spines of the third and forth vertebræ together form a thin, triangular lamina of bone, with sloping anterior and posterior margins, and a pointed distal extremity (fig. 56, *n.s.*^{3} and *n.s.*^{4}). The anterior margin and distal end of the lamina are suturally united to a thin vertical plate of bone which grows downwards from the long, backwardly directed supraoccipital spine (*so.′*). The spine of the fifth vertebra (*n.s.*^{5}) is unusually stout, and, moreover, is cleft distally into two processes, which are flattened on their opposed faces, and bent slightly outwards for the support of the anterior interspinous bones of the dorsal fin.

Each of the transverse processes of the fourth vertebra is greatly expanded, and also tilted slightly upwards from its root outwards (figs. 55 and 56, *tp.*^{4}). The root of the process is thick and flat, but for the distal two-thirds of its extent the process is comparatively thin, with its anterior and posterior margins curved downwards, whereby it becomes modified to form the roof and side walls of a transversely-disposed bony semicylinder, the cavity of which is open distally as well as proximally in the dry skeleton. The anterior margin not only curves downwards, but also a little backwards; the posterior margin is also decurved, but to a somewhat less extent than the former, and, with its distal extremity, which is prolonged outwards into a slender pointed process, is firmly united by suture to the anterior margin of the transverse process of the fifth vertebra. Proximally, as well as distally, the anterior and posterior walls of the bony semicylinder contract somewhat, and hence the enclosed recess becomes oval in shape in accordance with the contour of the contained air-sac. As in *Bagarius* the roof of the recess becomes so thin over a well-defined oval area as to be almost transparent. Two small foramina perforate the thick flat root of the process, and serve for the transmission of the rami ventrales of the fourth and fifth spinal nerves (fig. 55, *sp.n.*^{4}, *sp.n.*^{5}). The transverse process of the fifth vertebra (figs. 55 and 56, *tp.*^{5}) is unusually long and stout, with a free distal extremity, which is slightly recurved, and an anterior margin suturally articulated with the posterior margin of the preceding process. The origin of the process from the centrum, instead of from the neural arch like its predecessor, causes it to occupy a slightly more ventral position ; and, although not actually in contact with the air-bladder, it nevertheless helps to deepen the recess in which that organ is lodged. Its root is perforated for the passage of the ventral division of the sixth spinal nerve (fig. 55, *sp.n.*^{6}).

The superficial ossifications are but feebly developed in *Glyptosternum*. The sides of the centra of the first, the complex, and the fifth vertebræ are apparently somewhat thickened by superficial ossified deposit, but not continuously so, inasmuch as the intervertebral sutures are very evident, both on the lateral and ventral surfaces, and there is absolutely no trace of an aortic groove (fig. 55). On each of the ventro-lateral margins of the complex centrum there is a well-marked ventral ridge, and from this ridge, as in *Bagarius*, a thin, slender ventral process extends horizontally outwards to a point a little beyond, and ventrad to, the commencement of the oval recess enclosed by the modified transverse process of the fourth vertebra, and there terminates in a flattened and slightly expanded extremity (fig. 55, *v.p.*). At the junction of the flat root of the transverse process, with its more cylindrical distal portion, a slender spicule of bone (*d.l.*) grows downwards, and at its ventral extremity becomes firmly applied, if not actually anchylosed, to the dorsal or inner surface of the distal end of the ventral process. When the two processes meet, the vertical process gives off a slender prolongation, which passes horizontally forwards and a little downwards to articulate with a projection furnished by the free inner extremity of the decurved anterior margin of the transverse process (see left side in fig. 55, also in fig. 57). We have no difficulty in identifying the horizontally-disposed ventral process of *Glyptosternum* with the similarly situated process of *Bagarius*, and it is equally evident that the vertical process which meets its distal extremity is the equivalent of the dorsal lamina of other Siluroids. That the dorsal lamina in *Glyptosternum* does not reach the complex centrum is certainly peculiar, but it may be noted that its vertical and horizontal processes retain their normal relations to the posterior cardinal vein and the mesonephros, in that the latter structures pass between the former and the lateral surface of the complex centrum. The failure of the dorsal lamina to reach the complex centrum is exactly paralleled by a precisely similar arrangement in some other abnormal Siluroids (*e.g.*, *Clarias*).

The ascending process of the post-temporal (figs. 56 and 57, *pt.a.*) forms an expanded plate at each of the postero-lateral angles of the skull, articulating with the pterotic in front, and above with the epiotic and supraoccipital; the stem of the post-temporal slightly overlaps the anterior lip of the distal aperture of the bony semicylinder, and is further continued as a tubular prolongation containing the lateral line canal along the upper or dorsal lip. From the stem the inferior limb o the bone (figs. 55 and 57, *pt.i.*) extends inwards, at first, in contact with the anterior wall of the semicylinder, but, subsequently, separating therefrom, passes obliquely forwards to articulate with a lateral projection on the surface of the basioccipital. At the junction of the inferior limb with the stem, there is a deep groove which is almost completely closed behind by the distal extremity of the tubular transverse process, and converted into a socket for the clavicle (fig. 55). In a somewhat oblique lateral view of the hinder part of the skull and the modified anterior vertebræ (fig. 56), the relations of these structures to one another are clearly shown, including the formation of the posterior face of the skull by the supraoccipital, exoccipital, and epiotic bones; the convex dorsal surface of the tubular transverse process, and its close contiguity to the skull; as well as the extension of the stem of the post-temporal backwards to strengthen the anterior and dorsal margins of the distal aperture of the recess for the air-bladder. The slender head of the clavicle may also be seen projecting upwards through its tubular socket, near the distal extremity of the modified transverse process ($t.p.^4$), and between the latter and the inferior limb and stem of the post-temporal. On reference to fig. 57, a strong ligament may be seen passing from the distal extremity of the posterior process of the clavicle (*lgt.*, *cl.p.*) along the ventral margin of the lateral cutaneous area of its side to an insertion behind into the ventral surface of the transverse process of the fifth vertebra ($t.p.^5$).

In the outer wall of each auditory capsule, there is a deep basin-shaped depression of circular outline, the sides of which are formed by the prootic (fig. 55, *pr.o.*) and pterotic (*pt.o.*) in front, the pterotic and post-temporal (*pt.a.*) externally, the epiotic (*ep.o.*) and exoccipital (eo^2.) behind, and the prootic and opisthotic plate of the exoccipital ($e.o.^3$) internally, while the supraoccipital (*so.*) occupies the centre of the depression. Although a somewhat conspicuous feature in a lateral or ventral view of the external surface of the periotic capsule, this curious depression merely serves the purpose of affording an extensive surface of attachment for certain muscles connected with the branchial arches and pectoral girdle, but its internal effect is to render the utricular recess exceptionally shallow when viewed from the interior of the cranial cavity. Several of the otic bones, and more particularly the prootics, are so extremely thin as to be almost transparent, and the same remark applies also to the opisthotic plate of the exoccipital, especially where they form the external walls of the foveæ sacculi.

The foveæ sacculi, the cavum sinus imparis, and the atrial cavities appear to differ in no essential respect from the corresponding structures in other Siluridæ. The foveæ are, perhaps, somewhat larger than usual, while, on the contrary, the cavum sinus imparis is relatively smaller. Owing, it may be, to the large size of the foveæ, the cranial portion of the basioccipital is unusually wide, and, as the cavum and its atrial diverticula are relatively smaller than usual, the atria and their external apertures with the scaphia lie together within the cranial cavity and on the dorsal surface of the hinder part of the basioccipital. The large size of the foveæ also causes them to approach each other in the median line beneath the cavum sinus imparis, so that only a very thin vertical lamina of bone separates the two cavities.

As in *Bagarius* the air-bladder is completely constricted into two laterally situated oval sacs (fig. 57, *a.s.*). Each sac occupies and completely fills the central and similarly shaped portion of the recess enclosed by the modified transverse process of the fourth vertebra, and even projects ventrally beyond it, but nevertheless remains separated from the complex centrum by the length of the flattened root of the process. Externally the sac does not extend quite to the distal aperture of its bony recess, which to a slight extent is closed by the stem of the post-temporal, but principally by the lateral cutaneous area (*l.c.a.*) of its side.* The ventral surface of each air-sac is closely invested by the anterior portion of the mesonephros which, at the antero-internal angle of the sac, is prolonged inwards and then backwards, and, accompanied by the posterior cardinal vein, passes between the inner wall of the sac and the dorsal lamina externally, and the lateral surface of the complex centrum internally. The mesonephros in conjunction with a portion of the lateral lobe of the liver, also fills up the interval between the outer extremity of each air-sac and the inner surface of the corresponding lateral cutaneous area. The superficial coat of the air-bladder is but feebly developed, although it has skeletal attachments similar to those already described in the case of *Bagarius,* and may also be traced across the ventral surface of the complex centrum as it extends from the ventral surface of one air-sac to that of the other. The inner third of the under surface of each sac is overlapped by the distal portion of the ventral process (fig. 57).

The attachments of the walls of each air-sac to rigid portions of the skeleton are in the main similar to those of *Bagarius.* Thus, each sac is connected with the walls of its bony recess as follows:—(i.) along the dorsal edge of its posterior wall by an outer stratum of fibres which apparently becomes detached from the rest and is inserted into the posterior margin of the demi-cylindrical transverse process; (ii.) along the corresponding line of the anterior wall by the insertion of the dorsal edge of the latter into the decurved anterior margin of the same process; (iii.) the ventral wall is firmly attached to the distal portion of the ventral process; and (iv.) the inner wall is similarly adherent to the dorsal lamina and its horizontal prolongation.

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* The length of each sac is 4 mm. and the width 3 mm., the length of the Fish itself being five inches.

In the condition of the dorsal walls of the two air-sacs *Glyptosternum* exhibits an even more degenerate condition than what we believe to be the case in *Bagarius*, with the possible exception of a thin stratum of connective tissue investing the inner surface of the dorsal wall of each bony recess, which may represent the degenerate dorsal wall of the enclosed air-sac, the latter does not appear to be indicated by any definite stratum of fibres. We could detect no fibres derivable from the outer or anterior wall of the sac and converging in the dorsal wall towards the crescentic process of the tripus, although this ossicle retains its normal relations to the rest of the sac, and is easily seen in the usual position when the ventral wall has been removed. The dorsal edge of the anterior wall is wholly attached to the anterior margin of the tubular transverse process, and no fibres could be traced therefrom into the dorsal wall; an outer stratum of fibres in the posterior wall is similarly attached to the posterior margin of the same process, but the inner stratum thins away and disappears as a traceable layer without extending into the dorsal wall, as also is the case with the whole thickness of the outer wall. The inner wall, on the contrary, remains intact, and a few fibres are traceable therefrom to an insertion into the feebly concave inner margin of the crescentic process of the tripus. The latter fibres undoubtedly represent the remains of the characteristic radial fibres of other Siluridæ, and share with the remainder of the inner wall a fixed insertion into the dorsal lamina. In some instances we were able to detect a few fibres at the inner and posterior portion of the sac, which at one extremity were inserted into the distal extremity of the crescentic process of the tripus, and in the opposite direction were traceable into the adjacent portion of the posterior wall. It is possible that in such cases these fibres represent the sole remains of the triangular sheets of a normal air-bladder. In our description of a young *Bagarius* we referred to the existence of a few scattered fibres radiating outwards from the crescentic process of the tripus, forming an imperfectly fibrous dorsal wall to the air-sac, and subsequently extending into the anterior and antero-lateral walls. These fibres were so feebly developed that it is almost impossible to regard them as having any functional significance, and in older and more mature specimens, it is by no means improbable that they entirely atrophy, leaving each air-sac in a condition precisely similar to those of *Glyptosternum*.

We could detect no trace of any communication between the two air-sacs, or of the existence of a ductus pneumaticus.

The tripus is a triradiate ossicle, its three divergent divisions representing the anterior, articular, and crescentic processes (figs. 55 and 58, *tr.*). The anterior and articular processes (fig. 58, *tr.a.*, *tr.ar.*) are similar in shape, and of approximately equal length, and both taper towards their distal extremities. The crescentic process (*tr.c.*) is slightly longer than either of the other two processes, and although somewhat similar in shape has a faint inward curvature, but without forming the characteristic crescent. The concavity of the process is related to the dorsal lamina in such a way that it lies to the outerside of the latter, and at the same time partially encircles it (fig. 55). The scaphium has no ascending process, the small rounded condyle for articulation with the dorso-lateral edge of the centrum of the first vertebra being at the contracted posterior extremity of the spatulate process. The intercalarium is a very small nodule of bone imbedded in the interossicular ligament. The claustrum is either absent altogether, as appeared to be the case in one or two of our specimens, or, as in others, was apparently represented by a slender spicule of bone growing downwards from the lower border of the inclined neural arch of the complex vertebra towards the body of the first, and imbedded in the fibrous wall of the neural canal immediately behind the exoccipital.

As in *Bagarius* we had no difficulty in discovering a ductus endolymphaticus, but of a sinus endolymphaticus in the relatively small cavum sinus imparis we were unable to find any indication whatever. Our specimens of *Glyptosternum* were sufficiently well preserved to render our failure in the latter respect only explicable on the assumption that in this genus the sinus endolymphaticus has undergone complete suppression.

It is therefore obvious, from a comparison of the two forms, that as regards the condition of the air-bladder, and the nature of the associated skeletal modifications, *Glyptosternum* and *Bagarius* are in close agreement on all essential points, while differing to some extent in minor details, and further, that both are widely different from any of the normal species hitherto described. The better preserved condition of our examples of these genera enabled us to make a more satisfactory examination of the structure of the air-bladder and internal ear than was possible in the case of the similarly modified genera *Akysis* and *Acrochordonichthys*, and it may be worth while to institute a brief comparison between the former and those Siluridæ which possess air-bladders of the normal size and structure.

The more salient features in the air-bladders of *Bagarius* and *Glyptosternum* are clearly the result of degeneration, and can easily be conceived as due to the retrogressive modification of an originally normal organ. The two lateral air-sacs obviously represent the completely separated lateral halves of an ordinary anterior chamber longitudinally constricted from each other, the lateral compartments, always the most variable portion of the air-bladder in point of size, and the ductus pneumaticus having undergone total atrophy. No trace of the original communication between the two sacs persists unless a remnant of such a connection is to be found in the thin solid stratum of fibres which is continued from one sac to the other across the ventral surface of the centrum of the complex vertebra. But notwithstanding such indications of degeneration, it may be noted that the reduced air-bladder still retains the usual and normal attachments to fixed portions of the axial skeleton. Anatomically, at all events, the rigid skeletal attachments of each air-sac are capable of strict comparison with the similar connections of the walls of each half of a normal anterior chamber, more particularly as they occur in such Siluridæ as *Arius* and its allies. The attachment of the anterior and posterior walls of each sac to the corresponding margins of the modified transverse process of the fourth vertebra are respectively represented in *Arius pidada* for example, by the almost precisely similar skeletal attachments of the dorsal edges of the anterior wall of the anterior chamber, and of the primary transverse septum or posterior wall. The attachment of the mesial part of the dorsal wall of a normal anterior chamber to the ventral surface and sides of the complex centrum is apparently in part represented in both *Bagarius* and *Glyptosternum* by the sheet of fibres which extends from one air-sac to the other, and is at the same time firmly adherent to the ventral surface of the centrum in question, and which we cannot but regard as the consolidated mesial portion of an originally normal anterior chamber. If, as we have suggested, the dorsal ridge of *Bagarius* is the equivalent of the oblique lateral ridge of the complex centrum and the dorsal lamina of one side, the attachment of the inner wall of each air-sac to it might reasonably follow from the constriction of an originally normal anterior chamber into two laterally-placed sacs, and the consequent approximation of their anterior and posterior walls at the inner extremity of each sac. The same remark will apply also to *Glyptosternum*, although in this Siluroid the dorsal lamina is more easily recognised. The superficial coat of the air-bladder is obvious enough in both genera, but while it retains its normal attachments anteriorly to the decurved anterior margin of the transverse process of the fourth vertebra, the atrophy of the lateral compartments has enabled it to enter into a similar attachment posteriorly to the hinder margin of the same process. It is by no means improbable that the marked downward curvature of the anterior margin of this process is largely due to the actual ossification of that portion of the superficial coat which we have hitherto called the transverse membrane. The peculiar ventral process which, on each side, grows out from the ventro-lateral edge of the complex centrum may also, with some probability, be regarded as due to the extension of bony deposit from the superficial ossifications of the complex centrum into the superficial fibrous coat.

But while retaining in a fashion the usual rigid skeletal attachments the relations of the walls of the air-sacs to the movable tripodes afford further indications of the effects of degeneration. We entertain no doubt of the practical atrophy of the dorsal wall of each sac, and the almost complete disappearance of the usual strata of fibres by which, in the normal anterior chamber, the lateral and antero-lateral walls are functionally connected with the tripodes. With the suppression of these fibres the absence of the peculiar crescentic curvature in the posterior division of the tripus must be associated.

We shall subsequently have occasion to discuss these facts from a physiological point of view, and we shall now merely remark that in our opinion it is quite clear, from the partial enclosure of the two air-sacs within bony capsules, combined with the skeletal attachments of their anterior, posterior, and ventral walls, that no volumetric changes in the internal capacity of the sacs can possibly occur, except in the direction of the long axis of each through movements of its outer wall; and even if distension or contraction should take place in the latter direction, it is impossible that any motion could be imparted to the tripodes, by reason of the atrophy of the dorsal walls and the non-existence of the usual fibrous tracts by which such an effect is normally brought about. The extremely diminutive size of the air-bladder, when compared with the bulk of the Fish, taken in conjunction with such facts in the structure of the organ as those indicated above, force us to adopt the conclusion that the air-bladder in *Glyptosternum* and *Bagarius* must be regarded as a vestigial and functionless structure—a conclusion which receives additional support from the existence of similar retrogressive modifications in the Weberian mechanism, and in those parts of the internal ear that are specially related to it.

In our necessarily imperfect account of *Akysis* and *Acrochordonichthys* there were several interesting points that we were unable to determine with certainty, of which the most important were, the condition of the dorsal walls of the air-sacs, and the presence or absence of a sinus endolymphaticus. We cannot but think, however, that our tentative conclusions with regard to those genera derive considerable support from the results of our investigations of *Glyptosternum* and *Bagarius*. From the strong resemblance between the four genera in all essential osteological details, as well as in the general structure and skeletal attachments of their air-sacs, and in the condition of the Weberian ossicles, we now entertain but little doubt that, so far as *Akysis* and *Acrochordonichthys* are concerned, the agreement extends also to the atrophied condition of the dorsal walls, the suppression of the sinus endolymphaticus, and, in fact, to the rudimentary and functionless condition of both the air-bladder and Weberian mechanism.

Glyptosternum conirostris, STEINDACHNER.

We could detect no essential differences between this species and the preceding.

Euclyptosternum (sp. ?).

In an undetermined species of this genus given to us by Dr. DAY, we found the air-bladder and Weberian mechanism very similar in almost every detail to the corresponding structures in *Glyptosternum*.

Hara Buchanani.

We have had no opportunity of dissecting this Siluroid, but according to DAY (9) the air-bladder is "rather large and situated in the abdominal cavity, not enclosed in bone." It may, therefore, be concluded that the organ conforms to the normal Siluroid type.

Amblyceps (sp. ?).

The only reference to the air-bladder of this genus that we have been able to discover is by Day (9), who includes *Amblyceps* in his list of Indian Siluridæ in which the organ is "wholly or partially enclosed in bone."

Subfamily:—**SILURIDÆ STENOBRANCHIÆ.**

Group:—Doradina.

Ageniosus militaris.

There is a brief reference to the air-bladder of this species by Johannes Müller (28, fig. 10). The organ is said to be enclosed within a small osseous capsule formed by the "first" vertebra, which is open laterally, but divided in the median line by a bony partition wall. Two free blind diverticula from the bladder emerge posteriorly through two small apertures in the capsule.

From the division of its capsule into two cavities by an osseous partition, which is probably the centrum of the complex vertebra, it is highly probable that the air-bladder of *Ageniosus* is also constricted longitudinally into two laterally placed air-sacs, as in such forms, for example, as *Bagarius*, *Callomystax*, &c. The description is, however, too meagre to admit of detailed comparison with other types, but it may, nevertheless, be inferred, first, that the air-bladder of *Ageniosus* represents an abnormal and degenerate type, and secondly, that it bears a singular resemblance to the air-bladder of certain Cyprinidæ (*e.g.*, *Botia*) in which the partially atrophied posterior section of the organ is free in the abdominal cavity, while the anterior is more or less completely enclosed within a bony capsule.

Auchenipterus nodosus.

The only reference to the air-bladder of this species that we have been able to discover is by Johannes Müller. In a section of his valuable memoir (28) entitled "Ueber einen Springfeder-apparat zur Erweiterung der Schwimmblase bei mehreren Gattungen der Welse," Müller includes *Auchenipterus* among those Siluridæ that possess a peculiar "elastic spring" mechanism for the compression of the air-bladder, the importance of which he was the first to recognize, although Valenciennes had previously referred to its existence in his description of the skeleton of *Synodontis*. In figs. 5 and 6, Plate 3, of the memoir (*l.c.*) the "elastic spring" apparatus and its relation to the air-bladder are figured.

The centrum of the first vertebra (fig. 59, v') is much smaller than the centra of any of the normal vertebræ, but is nevertheless freely exposed both in the floor of the neural canal and externally on the ventral surface. The complex and three succeeding vertebræ are rigidly anchylosed together by the partial coalescence of their neural arches, but more especially by the superficial ossifications which continuously invest the lateral surfaces of their respective centra. The complex and fifth centra are about equal in length and width. The centra of the sixth and seventh vertebræ are much smaller, although larger than those of the free normal vertebræ which succeed them. The neural arch and short, thick spine of the third vertebra are both inclined forwards over the body of the first vertebra and partially anchylose with the exoccipitals and supraoccipital. The feeble spine of the fourth vertebra is directed obliquely backwards and supports the anterior interspinous bones of the dorsal fin, but is quite distinct from the preceding spinous processes. The remaining neural spines in the region of the dorsal fin, with the exception of the one belonging to the fifth vertebra are almost obsolete. The eighth vertebra is free and movable.

By a singular modification, each of the transverse processes of the fourth vertebra becomes converted into the "elastic-spring" apparatus of MÜLLER. The root of the process is a thin, highly elastic lamina of bone growing obliquely outwards from the neural arch and the backwardly inclined spine of its vertebra, and curving slightly downwards, with its anterior face looking obliquely upwards and forwards, and its posterior surface downwards as well as backwards (fig. 59, *t.p.*^{4}). At its distal extremity the root expands into an antero-posteriorly flattened oval plate, composed for the most part of loose, cancellous and almost friable bone (fig. 59). As the result of the ventral flexure of the elastic root the two surfaces of the plate look inwards and outwards respectively, but the slight obliquity of the plate gives to the inner surface a tendency to look downwards and backwards, and to the outer surface an upward and forward inclination. The outer surface of each plate is somewhat convex, and the curious concentric and radial striations which traverse it are so related to a point on the dorsal margin, near its anterior extremity, as to render the surface very similar in appearance to the external face and umbone of an inequilateral Lamellibranch shell. The inner surface, on the contrary, is faintly concave and has only the radial striations. Between the free ventral margin of each plate and the commencement of the flexible root, there is a deep, but narrow, slit-like groove into which the thin outer edge of the crescentic process of the tripus is received (*tr.c.*). The inner surfaces of the two plates are closely applied to thin oval areas in the antero-lateral regions of the anterior compartment of the air-bladder. A specialized portion of the dorso-lateral musculature of the body wall becomes separated from the rest to form a strong protractor muscle for each of the oval plates. This muscle has its origin on the external surface of certain bones forming the posterior face of the skull, viz.: the posterior plate of the exoccipital and the epiotic, and from thence is continued downwards and backwards to its insertion into nearly the whole extent of the external surface of the oval plate (fig. 61, *pt.m.*). By the contraction of this muscle each plate may be pulled outwards and upwards, the elasticity of its flexible root allowing such movement to take place, but at once compelling the plate to return to its previous position when the muscle ceases to contract. The transverse processes of the fifth vertebra (fig. 59, *t.p.*^{5}) are very rudimentary, being reduced to the condition of short, slender, spicular outgrowths. Like their predecessors they arise from the arch of their vertebra by thin obliquely set roots, and are widely separated both from the former and from the transverse processes of the sixth vertebra. The latter, with the ribs which they carry (*t.p.*^{6}, *r.*′), are more strongly developed than any that follow them, but are otherwise normal.

Thick superficial ossifications invest the lateral and ventral surfaces of the complex and two succeeding vertebral centra, but the sides only of the seventh centrum (fig. 59, *s.o.s.*). Beneath the centra of the complex, and the fifth and sixth vertebræ, the ossifications meet and blend in the median line to form the walls of a complete aortic canal (*a.c.*). Dorsally and laterally the ossifications do not extend on to the ventral surfaces of any of the transverse processes, but terminate in a sharp longitudinal ridge on each side which forms the inferior boundary of a groove for the posterior cardinal vein. Lateral ridge-like thickenings (*l.r.*) are developed on the sides of the anterior extremity of the complex centrum, and apparently mark the anterior limit of the superficial ossifications; these ridges coincide with the dorsal insertion of the median section of the transverse membrane, and also of a portion of the fibres forming the corresponding region of the anterior wall of the air-bladder. Radial nodules (*r.n.*) are represented by two elongated, slender nodules of bone lying along the lateral surfaces of the complex centrum at the dorsal extremities of the oblique lateral ridges, but united to the centrum by fibrous tissue only. There are no ossified dorsal laminæ.

The rigid connection of the anterior section of the vertebral column and the skull is secured by a peculiar development of dermal plates. The dorsal extremities of the two anterior interspinous bones are expanded into broad dermal plates, which are exposed on the dorsal surface behind the supraoccipital spine (fig. 61, *i.s.*^{1}, *i.s.*^{2}). The more anterior of the two (*i.s.*′) overlies the interval between the divergent spines of the third and fourth vertebræ, and articulates in front by a straight suture with the supraoccipital spine (*s.o.*′), and behind with the posterior plates (*i.s.*^{2}) by a concavo-convex suture, the two plates, with the greatly expanded spine of the supraoccipital, forming a strong bony armature for the dorsal region of the trunk behind the head. At each of the postero-lateral angles of the skull, and overlying the true epiotic element, there is a third dermal plate (*ep.o.*) wedged in between the ascending process of the post-temporal (*pt.a.*) and the pterotic (*pt.o.*) in front, and the supraoccipital and the two dermal interspinous bones behind and above, but having its outer margin free. From its posterior margin the dermal portion of the epiotic is prolonged backwards and downwards as a slender process of bone, which coincides with the superior margin of the lateral cutaneous area of its side, and serves for the anterior insertion of part of the dorso-lateral muscles of the body wall.*

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* As in *Glyptosternum*, the post-temporal, exoccipital, and epiotic bones form the walls of a deep basin-shaped depression near each of the postero-lateral angles of the cranium.

The post-temporal has the usual shape. The ascending process (fig. 61, *pt.a.*) suturally articulates with the dermal epiotic plate (*ep.o.*) and the pterotic (*pt.o.*) above, while the inferior limb (fig. 59, *pt.i.*), which is unusually stout, is firmly applied to a strong lateral outgrowth from the basioccipital (*bo.*). The inner surface of the stem, and the contiguous portion of the inferior limb, form between them a deep groove-like socket for the bifid head of the clavicle, but, as might be expected, no portion of the post-temporal has any articular relations with the flexible transverse process of the fourth vertebra. The posterior process of the clavicle (*cl.p.*) is strongly developed, and by its extension backwards marks the inferior boundary of the lateral cutaneous area of the same side.

The air-bladder is rather large in proportion to the size of the Fish, and broadly ovate in shape, with its anterior third somewhat contracted or pinched in by the application of the oval plates of the "elastic spring" apparatus to its lateral surfaces (fig. 60, *a.b.*). The walls of the bladder are very thin. Internally, the cavity of the organ is subdivided in the usual way into an anterior and two lateral compartments by primary transverse and longitudinal septa. The transverse septum (*t.s.*) is a fairly stout vertical pillar of fibres, continuous posteriorly with the longitudinal septum (*l.s.*). Dorsally, the transverse septum splits into two bundles of fibres, which pass on either side of the body of the sixth vertebra, and at the same time curve forwards as well as upwards to the ultimate insertions into the lateral surfaces of both the sixth and fifth centra. Through the narrowness of the septum, the apertures whereby the lateral and anterior compartments intercommunicate are unusually wide. The outer and posterior walls of the lateral chambers are strengthened internally by numerous vertically-disposed ridge-like aggregations of fibres, which are stoutest behind, but gradually become less marked as they are traced into the anterior chamber, where they finally disappear. There is no trace of secondary transverse septa. A ductus pneumaticus is present.

The attachments of the air-bladder, both to rigid and to movable portions of the skeleton, are substantially the same as in *Macrones*. The mesial section of the anterior wall of the bladder is attached dorsally to the ventral surface and oblique lateral ridges of the complex centrum, to the radial nodules, and also to the feebly developed ridges on the ventral surfaces of the crescentic processes of the tripodes. Externally to these attachments, and on each side, the fibres of the tunica externa have the same general arrangement in the lateral and antero-lateral walls as in *Macrones*, and converge in the dorsal wall in the form of triangular sheets to their ultimate connection with the tripodes (fig. 60). The thin median portion of the dorsal wall of the anterior chamber is restricted to that part which invests, and is firmly attached to, the lateral and ventral surfaces of the complex and fifth vertebral centra, inasmuch as, from the peculiar shape of the crescentic processes of the tripodes, and the absence of their usually widely open curvature, the oblique posterior margins of the triangular sheets are in close relation with those centra. Over a well defined oval area in each of the antero-lateral regions of the bladder the tunica externa becomes extremely thin, though still retaining its normal structure of an inner layer of vertically arranged fibres, and an outer stratum of curvilinear fibres. The thinness of these areas is principally due to the extreme tenuity of the outer stratum. The dorsal edges of the fibres forming each oval area are inserted into the outer rim of the thickened inner margin of the crescentic process of the tripus, immediately behind the insertion of the mesial fibres of the anterior wall into the ventral ridge of the same ossicle. To these oval areas the bony plates of the "elastic-spring" mechanism are so closely, and even forcibly, applied, that in all our specimens of this species the antero-lateral walls of the anterior chamber were distinctly pinched in (fig. 60).* Apart from a delicate connective tissue which extends between them, the oval areas are not specially attached to the bony plates; at all events, in spirit-preserved specimens the two structures readily separate from each other. The radial fibres of the tripus (*r.f.*) are somewhat feebly developed, and, from the peculiar shape of the crescentic process of that ossicle, pursue an almost straight course forwards as they pass from the latter to their connection anteriorly with the radial nodule.

A thin transversely-disposed membrane is closely applied to the proper anterior wall of the bladder, and is attached dorsally to the lateral ridges of the complex centrum; laterally to this the membrane becomes continuous with the margins of each oval plate of the "elastic spring" mechanism, and from thence becomes lost on the lateral and ventral surfaces of the bladder.

In shape, the tripus (fig. 59, 62 and 63, *tr.*) is very unlike that of most other Siluridæ, although it possesses the three characteristic divisions. The ossicle is almost straight, the posterior or crescentic process (*tr.c.*) being almost a direct continuation backwards of the anterior process (*tr.a.*), with not more than the faintest suspicion of the usual inward curvature. Both processes are much flattened, but the crescentic process is almost twice the length and width of the anterior division (fig. 62). The ventral surface of the root of the crescentic process is traversed by a faint oblique ridge (*v.r.*); the outer margin is extremely thin, and fits into a slit-like groove at the junction of the oval plate with the flexible root of the "elastic spring" apparatus (fig. 59, *tr.c.*); the inner margin, on the contrary, is curled inwards on itself, so as to form a thickened rim on the ventral surface, and, moreover, is somewhat longer than the outer margin (fig. 62). As previously mentioned, the ventral ridge of the tripus receives the insertion of a slip of fibres derived from the median portion of the anterior wall of the bladder; the thickened inner rim of the crescentic process, receives on its inner edge the insertion of the radial fibres from the radial nodule; while the outer margin of the rim has attached to it from before backwards, first, the dorsal edges of the fibres derived from the corresponding antero-lateral wall of the anterior chamber and traversing one of the thin oval areas, and, secondly, the fibres primarily derived from the remaining portion of the lateral wall, as well as those converging from the outer wall of the lateral compartment of the same side. The thin outer rim of the crescentic process does not receive the insertion of any of these fibres, as the latter simply cross its ventral surface on their way to the thickened inner rim, which is consequently the only portion of the tripus that can be seen imbedded in the dorsal wall of the bladder after the removal of the tunica interna (fig. 60, *tr.c.*). The unusual length of the crescentic process seems to be associated with the relatively large size of the anterior chamber, and also with the fact that the process not only receives the insertion of the fibres derived from the antero-lateral and lateral walls of the anterior chamber, but also from the outer wall of the contiguous lateral compartment. The absence of any marked curvature in the process may also have conditioned its somewhat exceptional length. At the junction of its anterior and crescentic processes a thin, flexible, and highly elastic, triangular lamina of bone is given off from the dorsal surface of the tripus and at right angles to it (fig. 63, *tr.ar.*). The surfaces of the lamina look almost directly backwards and forwards respectively, and the inner margin, from its junction with the body of the tripus to the pointed dorsal extemity of the lamina, is confluent with the neural arch of the complex vertebra along a line which is slightly oblique from below upwards and forwards. This lamina undoubtedly represents the articular process of other Siluroids, from which, however, it differs in being directly continuous with the neural arch instead of articulating with the lateral surface of the centrum at the bottom of a deep pit-like socket. Consequently the movements of the tripus in *Auchenipterus* will not depend on a normal articulation, but solely on the flexibility and elasticity of its peculiar articular process. Then again, in most Siluridæ with normal bladders, it is the radial fibres of the tripus which cause that ossicle to move inwards towards the complex centrum when the lateral distension of the anterior chamber has ceased to separate the two, but in *Auchenipterus* the function of the radial fibres, which, from their relatively feeble development and nearly straight antero-posterior course, is possibly less efficient than in other Siluroids, must be powerfully supplemented by the elasticity of the articular process. As in all probability the tripus is to be regarded as the modified transverse process of the third vertebra it will at once be obvious that it presents a striking resemblance to the corresponding process of the fourth vertebra. In each case there is a flexible and elastic root directly continuous with the neural arch of its vertebra and in distal continuity with a movable plate of bone—the body of the tripus in the one case and the oval plate of the "elastic-spring" apparatus in the other. The fact may also be recalled that as regards the thinness of its root and the curious obliquity of its origin from the neural arch the transverse process of the fifth vertebra, although neither flexible nor elastic, strongly resembles the two preceding processes.

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* SÖRENSEN'S conclusions (37) with regard to *Doras* and *Synodontis*, viz., that the oval plates of the "elastic-spring" apparatus owe their formation to the ossification of "la plèvre" (= the transverse membrane) and the tunica externa of the bladder itself, may be extended also to *Auchenipterus*. The relations of the transverse membrane to the terminal plates in this genus, and the extreme tenuity of the walls of the bladder where the plates are applied to them, are quite in harmony with this suggestion.

In reference to the movements of the tripus it seems to us not improbable that the relation of its crescentic process to the slit-like groove between the oval plate and the elastic root of the transverse process of the fourth vertebra must also, to some extent, limit and control the lateral motion of that ossicle, even if it does not altogether prevent the possibility of any such movement, when the protractor muscle is quiescent and the plates are not pulled outwards and upwards. On the other hand, the contraction of these muscles, and the consequent upward and forward movement of the plates, will necessarily confer upon the tripodes a wider range of possible lateral motion. In fact, as we shall subsequently have occasion to point out more in detail, any increase in the volume of the anterior chamber of the air-bladder will mainly depend on the movements of the oval plates in the way just described, but it is precisely such movements that will give to the tripodes an increased range of lateral motion, and, at the same time, the capacity for registering the degree of distension of the bladder. Conversely, the compression of the air-bladder by the elastic recoil of the plates when their protractor muscles cease to contract, will necessarily have the effect of confining the movements of the ossicles within comparatively narrow limits.

In the general structure of the various parts of the internal ear, and of the recesses in which they lie, *Auchenipterus* closely agrees with *Macrones.*

Lateral cutaneous areas are well marked, but the oval plates of the "elastic-spring" mechanism, to a large extent, prevent the lateral walls of the anterior chamber from coming into direct contact with them, but behind the plates the lateral walls, and to some extent the outer walls of the lateral compartments also, are in close relation with these areas. The spaces between the plates and the superficial skin are occupied partly by the large protractor muscles, and partly by a yellowish fatty tissue.

Auchenipterus obscurus.

But for one or two minor points of difference, this species very closely resembles the preceding one. The superficial ossifications are somewhat more extensively developed, inasmuch as they extend on to and invest the lateral surfaces of the eighth vertebral centrum, so that the ninth is the first of the flexibly articulated series. A further distinctive feature is to be found in the presence of a small cæcal diverticulum which is given off from the posterior and outer extremity of each of the lateral compartments of the air-bladder.

Euanemus.

Since JOHANNES MÜLLER (28) first recorded the existence of an "elastic-spring" apparatus in this South American genus, the relations of the mechanism to the air-bladder have been carefully described by SÖRENSEN (37) in *E. nuchalis.*

Instead of each terminal disc or plate being flat on its posterior face, or only slightly concave, it is hollowed out in the form of a pouch. The formation of these singular structures and their relations to the tunica externa of the air-bladder are thus described by SÖRENSEN :—" la membrane externe de la vessie natatoire est ossifiée en dehors (ou en avant), et en haut, au bord du disque, l'ossification s'étend dans toute son épaisseur, tandis que, près du bord supérieur dudisque, cette membrane n'est ossifiée sur la face interne (ou postérieure) que dans une petite étendue." (*Loc. cit.*, pp. 139–140.)

Cetopsis candira.

Cetopsis is one of the nine genera of Siluridæ in which JOHANNES MÜLLER (28) denied the existence of an air-bladder, and his statement on this point remained uncorrected until it was shown by one of us (4) that in *C. candira* the organ is undoubtedly present in a diminutive and bone-encapsuled condition. The description then given may now be supplemented in one or two minor features.

Cetopsis differs from all other Siluridæ with which we are acquainted in that the neural arch of the complex vertebra is not perforated by a single foramen for the passage of the roots of spinal nerves. The second to the fourth, inclusive, emerge between the exoccipital and the arch of the complex vertebra, the last-mentioned nerve traversing a slight notch in the anterior margin of the arch. The fifth nerve escapes between the arches of the complex and fifth vertebræ, while the sixth and remaining spinal nerves perforate in the normal fashion the arches of the fifth and succeeding vertebræ.

The transverse processes of the fourth vertebra are alone concerned in the formation of the osseous capsules for the enclosure of the rudimentary air-bladder, and are represented on each side by a hollow bony cylinder disposed at right angles to the long axis of the vertebral column. The formation of each cylinder is apparently due to the expansion of the transverse process combined with the downward curvature of its anterior and posterior margins, and their subsequent fusion on the ventral surface. The distal aperture of the cylinder is closed by the external skin and a deposit of subcutaneous fatty tissue, and to a slight extent also by the lateral musculature of the trunk. Proximally, the cylinder is continuous with the centrum and arch of the complex vertebra. Near its junction with the vertebra each cylinder is slightly bullate on its dorsal surface, but for the rest of its extent is of fairly uniform calibre. The bony walls of the cylinders are everywhere complete except at their distal extremities. Two foramina perforate the root of each cylinder, one on the ventral surface and the other in the anterior wall, both apertures being close to the junction of the cylinder with the complex vertebra; the first serves for the transmission of the ventral divisions of the second, third and fourth spinal nerves, while the second admits of the passage of the tripus from the interior of the cylinder to its connection with the scaphium anteriorly. The transverse processes of the fifth vertebra have no share in the formation of the osseous capsules for the air-bladder, nor do they in any way differ from the normal rib-bearing processes that succeed them.

Except for the slenderness of its inferior limb the post-temporal is normal, and with the distal portion of the cylindrical transverse process forms the articular cavity for the clavicle.

The air-bladder is constricted into two small, extremely thin-walled, laterally placed, oval air-sacs, which occupy the slightly inflated proximal portions of the two bony cylinders. Each sac in a Fish 8 inches long was only 6 mm. in length, but, nevertheless, had structurally perfect walls. The walls of each sac are in close relation with those of its investing bony capsule, without, however, being specially attached thereto, except at one point where the inner wall is adherent to the lateral surface of the complex centrum. The solitary specimen examined by us had been eviscerated before dissection, but a most careful examination failed to reveal the existence of any communication between the two sacs, or of any trace of a ductus pneumaticus.

A scaphium without either condylar or ascending processes is present, but neither intercalaria or claustra could be detected. The tripus is very similar to that of *Bagarius,* except that it has only the barest rudiment of a straight "crescentic" process for insertion into the antero-internal portion of the dorsal wall of the corresponding air-sac. No obviously specialized radial fibres could be made out, but are probably represented by that part of the inner wall of the air-sac which is attached to the complex centrum. There are no radial nodules.

The cavum sinus imparis and the atrial cavities appeared to be perfectly normal, but relatively of small size. Unfortunately, the auditory organ was too badly preserved to admit of a satisfactory examination of its structure being made.

Doras maculatus.

The existence of an "elastic-spring" apparatus in this South American species was first described by JOHANNES MÜLLER (28), but a more detailed account of the relations of the mechanism to the walls of the air-bladder has recently been given by SÖRENSEN (37, Plate 2, figs. 15, 16). In an earlier paper by the same author (36, Plate 3, fig. 44, and Plate 4, fig. 43), the bladder itself is figured.

From SÖRENSEN'S figures it would appear that as regards its skeletal modifications, and the mode of formation and relations of its "elastic-spring" mechanism, *Doras* exhibits a fairly close resemblance to *Auchenipterus* and *Oxydoras* in all essential features. The thick discoidal terminal plates of the mechanism are closely applied to the antero-lateral regions of the bladder. There seems to be no recognisable posterior division to the transverse process of the fourth vertebra, and the fifth vertebra has but a pair of rudimentary processes which are widely separated from those of the fourth and sixth (*loc. cit.*, Plate 2, figs. 14–16).

The air-bladder is partially constricted into two portions, of which the anterior is cordate in shape, and subdivided internally into the usual anterior and lateral compartments by transverse and longitudinal septa (*loc. cit.*, Plate 4, fig. 43). The posterior portion (*loc. cit.*, Plate 3, fig. 44), is a long internally sacculated cæcal appendage, closely resembling the corresponding structure in *Malapterurus.* Unlike all other Siluridæ in which an "elastic-spring" mechanism is present, the anterior chamber is fringed on each side by a series of variously-sized more or less branched, tubular cæca. Over the circular or somewhat oval areas, where the terminal discs of the two elastic springs are applied to the walls of the anterior chamber, only the thin, delicate, transparent tunica interna is present. On this point, and with reference to the mode of formation of the discs, SÖRENSEN (*loc. cit.*, p. 139) remarks:—" Chez le genre *Doras*, il* se termine en un disque rond et épais qui est une ossification de (la plèvre et de) la membrane externe de la vessie natatoire dans toute son épaisseur, de sorte qu'en ouvrant la vessie natatoire on aperçoit ce disque à travers la membrame interne pellucide." According to SÖRENSEN, therefore, the thickened discs in which the transverse processes of the fourth vertebra terminate distally are to be regarded as owing their formation to the extension of ossification from the transverse processes into the transverse membrane (la plèvre), and the whole thickness of the tunica externa.

The crescentic process of the tripus (*loc. cit.*, fig. 15) has apparently the same shape as in *Auchenipterus.*

Oxydoras brevis.

We are not acquainted with any previous reference to the air-bladder of *Oxydoras*, nor are we aware that the presence of an "elastic spring" apparatus in this genus has hitherto been recorded.

In all essential features the modified anterior vertebræ and their processes are similar to those of *Auchenipterus nodosus.* The transverse processes of the fourth vertebra are modified to form an " elastic spring " mechanism. The deflected distal portion of each process (fig. 64, *t.p.*^{4}) forms, however, but a slightly expanded and inwardly curved plate with a thickened outer margin and an almost nodular extremity. Near the junction of each plate with its elastic and flexible root there is a slight groove into which the outer margin of the crescentic process of the tripus is received. As in *Auchenipterus*, the modified transverse process has no trace of a posterior division, but, unlike that genus, the fifth vertebra has scarcely any trace of transverse processes, and, as is usually the case where the lateral surfaces of the body are protected by an armature of dermal bony plates (*e.g.*, the Loracaroid Siluridæ), the first pair of ribs are exceptionally massive. The radial nodule (*r.n.*) is an elongated spicule of bone, somewhat loosely attached by fibrous tissue to the lateral surface of the complex centrum.

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* The transverse process of the fourth vertebra.

Its slightly thickened dorsal extremity is almost in contact with the inner margin of the root of the crescentic process of the tripus (*tr.c.*), with which it is connected by a few short radial fibres. The inferior limb of the post-temporal (*pt.i.*) is very massive, and articulates internally with the basioccipital (*bo.*), and along its dorsal edge with the angle which the posterior and opisthotic plates of the exoccipital make with each other at the postero-lateral region of the skull.

The air-bladder (fig. 66) is also very similar in shape and relative size to that of *Auchenipterus.* The anterior chamber (*a.c.*) is fairly large, and its lateral walls are in close and extensive contact with the superficial skin. The transverse septum (*t.s.*) is attached dorsally to the body of the fifth vertebra, and anteriorly to this to a longitudinal ridge which traverses each of the lateral surfaces of the complex centrum and marks the dorsal limit of the superficial ossifications, and also coincides with the inner margin of the corresponding triangular fibrous sheet of the dorsal wall of the anterior chamber. The lateral portions of the anterior wall of the bladder are extremely thin and translucent where the distal plates of the "elastic spring" mechanism are applied to them, in fact, the latter project into the cavity of the anterior chamber, pushing in the thin wall of the bladder before them. At the point of closest contact of the two structures the tunica externa is entirely wanting, and only the thin inner tunica invests the inwardly projecting extremities of the two plates.* The peripheral margins of the plates are somewhat firmly attached to the wall of the bladder by connective tissue. The posterior extremity of the bladder has a small rudiment of a posterior cæcum (*p.c.*) sub-divided internally by a backward prolongation of the longitudinal septum which, anteriorly, separates the two lateral compartments from each other.

The Weberian ossicles are much the same as in *Auchenipterus.* The crescentic process of the tripus (fig. 65, *tr.c.*) is, however, shorter than the anterior process (*tr.a.*) and without a trace of any inward curvature. From the manner in which the fibres of the dorsal wall of the anterior chamber are connected with it the crescentic process appears somewhat triangular in shape when viewed from the ventral surface after the removal of the tunica interna (fig. 66). The articular process (*tr.ar.*) is a thin flexible lamina of bone, continuous with the arch of the complex vertebra, and in correlation with this modification the radial fibres are so feebly developed as to be almost non-existent.

Synodontis schal.

JOHANNES MÜLLER (28) has figured and described the "elastic-spring" apparatus of this African Siluroid and its relations to the air-bladder (*loc. cit.*, Plate 3, figs. 1 to 4). SÖRENSEN, in his paper "Om Lydorganer hos Fiske," also gives an external lateral view of the air-bladder of *Synodontis* with the object of showing the relations of the

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* These facts suggest that in the mode of formation of the nodular terminal plates of the mechanism *Oxydoras* resembles *Doras*, *Synodontis*, and *Auchenipterus.*

"elastic-spring" mechanism to the walls of that organ. We regret that we have only been able to examine a skeleton of this species, but we venture to give a brief description of certain features in its structure for the sake of comparison with other types. It is interesting to remark that in many of its skeletal details *Synodontis* exhibits a much closer resemblance to the East Indian genus *Pangasius* (*e.g.*, *P. Buchanani*, *P. djambal*) than to those South American Siluroids in which an "elastic-spring" apparatus is present.

The first, the complex (fig. 67, *c.c.*), and the fifth ($v.^5$), and sixth ($v.^6$) vertebræ are rigidly connected together by investing superficial ossifications which continuously thicken the ventro-lateral surfaces of their centra, and terminate in front at the anterior end of the complex centrum in strong oblique lateral ridges that overlap the basioccipital, or rather articulate with its thickened ventral portion by an interdigitating suture. The true body of the first vertebra is therefore not visible externally on the ventral surface. There is a deep aortic groove (*a.g.*). Stout radial nodules (*r.n.*) are attached to the oblique lateral ridges of the complex centrum, and fairly broad dorsal laminæ (*d.l.*) extend therefrom ventrad to the cardinal grooves, and blend with the ventral surfaces of the posterior divisions of the transverse processes of the fourth vertebra. Unlike *Auchenipterus*, *Doras*, and *Oxydoras*, each of these processes in *Synodontis* is deeply cleft into anterior and posterior divisions, of which the latter ($tp.^4p.$) is directed obliquely backwards and acutely pointed at its free distal extremity, while the former is modified to form an "elastic spring" mechanism. The anterior division ($tp.^4a.$) has an oblique origin from the arch of the complex vertebra, continuous behind with the flat but much stouter root of the posterior division, and, after extending slightly forwards, and, at the same time, curving downwards, becomes bent backwards on itself, and expanded into a flattened and somewhat semicircular plate, the posterior surface of which is directed backwards and a little upwards (fig. 67). The anterior face of the plate is strengthened by a stout projecting process which extends forwards and upwards over the inferior limb of the posttemporal (*pt.i.*), and probably serves for the insertion of the protractor muscle of the mechanism. From their position and the direction of their faces these plates must have been applied to the lateral portions of the anterior wall rather than to the antero-lateral or lateral walls of the anterior chamber as is the case with *Auchenipterus*.* The transverse processes of the fifth vertebra ($t.p.^5$) articulate with the basal portions of the posterior divisions of the preceding processes by irregular interdigitating sutures, but otherwise form long triangular structures, directed obliquely backwards and pointed at their free distal extremities. Those belonging to the sixth vertebra (*t.p.*^{6}) are widely separated from the foregoing, and carry the first pair of ribs. As the transverse process of the fourth vertebra contributes nothing to the support of the pectoral girdle, the inferior limb of the post-temporal (*pt.i.*) is unusually massive, and articulates internally with an equally stout outgrowth from the lateral surface of the basioccipital. For the same reason, and as in *Auchenipterus* and *Oxydoras*, the ascending process of the same bone has an extensive and intimate articulation with the dermal nuchal plates, and with the skull.

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* With regard to the terminal plates of the mechanism and their relations to the wall of the anterior chamber, it will be seen from the following extract from SÖRENSEN's more recent paper (87, p. 140), that *Synodontis* closely agrees with *Doras*:—"Chez le genre *Synodontis*, le disque peu épais du ressort est une ossification de la couche externe de la membrane externe; la couche interne est ici assez mince et s'étend le long de la face interne (postérieure) du disque, dont elle est séparée par une masse épaisse gélatineuse d'une nature particulière."

The tripus is normal. The crescentic process (*tr.c.*) rests upon the flexible root of the "elastic-spring" of its side, and describes a somewhat sharp, inward, and downward curvature along, and in contact with the contiguous lateral surface of the complex centrum. The posterior margin of the process is deeply grooved for the attachment of the converging fibres of the dorsal wall of the anterior chamber, while its ventral surface is traversed by an exceptionally well-marked ventral ridge. The depth of the groove and the strength of the ridge suggest that the air-bladder of this species is furnished with unusually stout walls. It is not so obvious as in *Auchenipterus* and *Oxydoras* that the movements of the tripodes in *Synodontis* can, to any great extent, be limited or controlled by the action of the "elastic-spring" apparatus. Except that the ascending process is very short the scaphium is normal. The intercalarium is a small oblong nodule in the usual position.

GROUP :—RHINOGLANINA.

Callomystax gagata.

In this Indian Siluroid, we again meet with an example of that abnormal type of air-bladder in which the organ is longitudinally constricted into two simple lateral air-sacs, and more or less completely enclosed within bony capsules formed by the modified transverse processes of certain of the anterior vertebræ. But although *Callomystax* bears a general resemblance to such Siluroids as *Glyptosternum*, *Bagarius*, and others, in these respects it is, nevertheless, not without certain noteworthy peculiarities of its own. It is this species that possesses the peculiar modification of the confluent spinous processes of the fourth and fifth vertebræ, and the first and second interspinous bones of the dorsal fin to form a stridulating mechanism, which has already been described by one of us.* Beyond a brief reference to the air-bladder by DAY (9), who includes the genus under the name *Gagata*, in his list of those Indian Siluridæ, in which the organ is said to be partially or completely surrounded by bone, we are not aware of any recorded observations.

The complex and fifth vertebræ are rigidly connected with each other by the anchylosis of their neural arches and spines, and also with the skull by the firm sutural union of the arch and spine of the third vertebra with the supraoccipital and the exoccipitals, and by a similar union of the transverse processes of the fourth vertebra with the post-temporals. The body of the first vertebra (fig. 70, *v.*^{1}) is unusually small, being represented by a thin discoidal bone firmly wedged in between the basioccipital and the complex centrum. Its ventral surface is visible externally, but dorsally the centrum is partially excluded from the floor of the neural canal by the conjoined margins of the complex centrum and basioccipital. The complex centrum (*c.c.*) is more than twice the length of the centrum of the fifth vertebra (*v.*^{5}), which in turn is but a little larger than one of the succeeding free normal centra. The sixth vertebra is normal and freely movable on the foregoing. Owing to the width of the intervertebral ligament between the fifth and sixth centra, and the complete freedom of the arch and spine of the latter, there is considerable lateral and vertical mobility between the sixth and remaining trunk vertebræ and the fifth and preceding vertebræ.

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* A. C. HADDON, "On the stridulating apparatus of *Callomystax gagata*."—'Journ. Anat. and Physiol.,' vol. 15, p. 322 (17A).

The spinous processes of the third, fourth, and fifth vertebræ (fig. 68, *n.s.*^{3}, *n.s.*^{4}, and *n.s.*^{5}) are confluent, and together form a high, laterally compressed lamina of bone, with an oblique backwardly projecting posterior margin, a dorsal edge which is somewhat rounded behind but slopes downwards in front, and a relatively short anterior margin. The anterior portion of the plate, representing the spine of the third vertebra, is inclined forwards and, with the neural arch with which it is continuous inferiorly, firmly articulates with the supraoccipital and exoccipitals, and also along its dorsal border with a descending process derived from the supraoccipital spine (*s.o.*^{1}). The posterior section of the lamina, representing the spines of the fourth and fifth vertebræ, and separated from the anterior by a well marked semicircular notch in the dorsal margin, is longitudinally cleft to its root into two thin opposed plates* separated by an interval sufficiently wide to receive the modified first and second interspinous bones of the dorsal fin (*i.s.*,^{1} and *i.s.*^{2}). The inner surface of each of the two opposed plates is transversed by a series of closely set, vertically arranged and parallel ridges while the first interspinous bone is similarly ridged on both its surfaces like a double file. The vertical flexure of the sixth and succeeding vertebræ on the anterior rigidly interconnected vertebræ will necessarily cause the ridges on the interspinous bone to scrape against those on the inner surfaces of the cleft neural spines, and therefore probably lead to the production of more or less acute voluntary sounds.

The transverse processes of the fourth and fifth vertebræ combine on each side to form a hollow, transversely disposed and somewhat shallow bony funnel, the mouth of which is slightly expanded and closed only by the lateral cutaneous area of its side, while the somewhat contracted proximal extremity is continuous with the centra and neural arches of the vertebræ in question (fig. 68). The greatly expanded transverse process of the fourth vertebra (figs. 68 and 70, *t.p.*^{4}), which forms the greater part of each funnel, is tilted upwards and its anterior margin bent downwards in close contact with the inferior limb of the post-temporal (fig. 70, *pt.i.*), and then backwards, so as almost to meet the anterior edge of the transverse process of the fifth vertebra, thereby forming the anterior and ventral as well as the dorsal walls of the funnel. The recurved lamina forming the incomplete ventral wall (fig. 70, *t.p.*^{4}) is extremely thin besides being interrupted by two considerable vacuities which are normally filled in by a thin but tough fibrous membrane. Its outer edge forms the lower lip of the mouth of the funnel (fig. 68), and its inner margin is confluent with the ventro-lateral edge of the complex centrum (fig. 70), so that what is a cleft for the passage of the tripus from the air-bladder to the scaphium, in *Bagarius* and *Glyptosternum*, becomes converted into a complete foramen in *Callomystax*. The bony margins of the two vacuities, as well as the inferior lip of the distal opening of the funnel, have a peculiar indentated or crenulated outline. The posterior margin of the transverse process is also decurved (fig. 68) and articulates by an almost obliterated suture with the dorsal surface of the transverse process of the fifth vertebra (*t.p.*^{5}), and, with the latter, forms the posterior wall of the funnel. It will be apparent, therefore, that the transverse process of the fourth vertebra constitutes the dorsal, anterior ventral, and part of the posterior wall of each funnel, while the transverse process of the fifth vertebra completes the posterior wall, and further, that the cavity of the funnel is closed distally by the corresponding lateral cutaneous area, and proximally by the lateral surface of the complex centrum, except at its antero-internal extremity where a small foramen admits of the passage of the tripus from the interior of the funnel to its connection with the scaphium anteriorly. The transverse process of the fifth vertebra (figs. 68 and 70, *t.p.*^{5}) is unusually long and massive, with a slight ventral inclination. Its dorsal surface suturally articulates with the decurved posterior margin of the preceding process, but its anterior margin is separated by a vacuity from the ventral wall of the funnel (fig. 70).

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* In the paper on the stridulating mechanism referred to above the two plates are said to be formed by the vertical division of the neural spines of the coalesced anterior vertebræ, but more precisely, and as here stated, they represent the confluent and cleft spines of the fourth and fifth vertebræ.

The otherwise imperfect ventral wall of each funnel is completed by a thin fibrous membrane which extends between the crenulated margin of the transverse process of the fourth vertebra and the anterior margin of the transverse process of the fifth vertebra, and is also continued across the ventral surface of the complex centrum from one funnel to the other. There is no trace of the peculiar ventral processes of *Bagarius*, *Glyptosternum*, or *Clarias*.

The superficial ossifications do not, to any obvious extent, thicken the lateral surfaces of the centra of the complex and fifth vertebræ, nor do they form an aortic groove or canal, although as a thin layer of bony deposit they obliterate any external indication of the intervertebral suture between the two centra, except on the ventral surface. At the inner extremity of each funnel-shaped recess, and near the inner lip of the foramen through which the tripus is connected with the scaphium, there is a small radial nodule attached to the lateral surface of the complex centrum. No dorsal laminæ could be made out, nor any obvious grooves for the posterior cardinal veins.

The stem and ascending process of each post-temporal (fig. 68. *pt.s.* and *pt.a.*) have a somewhat curved posterior margin which strengthens, and to some extent deepens, the mouth of the funnel at its anterior and dorsal edges. The inferior limb (fig. 70, *pt.i.*) has the usual articulation with the lateral surface of the basioccipital, and for a part of its extent is firmly applied, if not actually anchylosed, to the anterior wall of the funnel. The socket for the clavicle (*cl.s.*) is formed by a groove between the stem and inferior limb of the post-temporal, which is completely closed posteriorly by the distal margin of the anterior wall of the funnel-like transverse process.

As in *Glyptosternum* and *Auchenipterus* the outer surface of each auditory capsule is marked by a deep cup-shaped depression.

The air-bladder (figs. 68 and 70, *a.s.*) is reduced to the condition of two thin-walled, laterally situated air-sacs, which occupy the cavities of their respective bony funnels. Each sac is nearly spherical in shape but slightly contracted at the inner extremity where it is in relation with the tripus. Laterally, the sac bulges outwards into the wider portion of its funnel and has its outer wall nearly, if not actually, in contact with the inner surface of the adjacent lateral cutaneous area.* In fresh specimens, or when the air-sacs are not shrunken by the action of preservative fluids, it is probable that the two sacs are closely and extensively applied to these areas. Each sac is sufficiently large to be in close contact on all sides, except the outer wall, with the inner surface of its investing bony capsule, but with the exception of the inner wall no fibrous connection between the two could with certainty be made out. In one of our two specimens of *Callomystax* we noticed that the two air-sacs were not symmetrically developed. The one on the right side had extremely thin and almost transparent walls, and appeared also to be somewhat the larger of the two, its outer wall being closely applied to the lateral cutaneous area of its side. The left sac had much thicker and more opaque walls, and, from its smaller size, the outer wall was widely separated from the external skin.

We could discover no communication between the two air-sacs, neither were we able to detect any trace of a ductus pneumaticus.

An examination of the structure of the walls of the two sacs at once shows that in the arrangement of their component fibres, and in the relations of the latter to the tripodes, each sac is substantially similar to the lateral half of an anterior chamber in a normal air-bladder. The crescentic process of the tripus is imbedded in the dorsal wall of the sac near to its anterior and inner extremity, and the fibres radiating from the convexity of the process form, as usual, an inner and an outer stratum. The fibres of the outer stratum pursue the normal curvilinear course in passing from the tripus into the dorsal, antero-lateral, and lateral or outer walls; the fibres of the inner stratum have exactly the same attachment and distribution, but radiate directly outwards from the tripus. The two strata are of uniform thickness over the greater part of the dorsal wall of each sac, and together may be taken as representing one of the triangular sheets of a normal anterior chamber, but along a somewhat sharply defined line extending from the posterior or inner extremity of the crescentic process of the tripus, obliquely outwards and backwards to the outer margin of the posterior wall of the sac, the dorsal wall becomes extremely thin, resuming, however, its normal thickness as it subsequently extends downwards to form the posterior wall. This thin area probably corresponds to one half of the thin medio-dorsal portion of the tunica externa in a normal and undivided anterior chamber, and both it and the dorsal edge of the posterior wall appeared to be slightly adherent to the skeleton along an oblique line coincident with the posterior margin of the transverse process of the fourth vertebra. This adhesion of the posterior wall to the skeleton is evidently the equivalent of the dorsal attachment of the primary transverse septum in the normal bladder. The fibres forming the inner wall of each sac are attached dorsally to the feebly developed radial nodule, and, towards the anterior wall, to the ventral surface of the tripus near the root of its crescentic process; these fibres represent what in other Siluroids we have termed the "anterior pillars." Radial fibres converge from the crescentic process to the radial nodule in the usual manner.

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* The antero-posterior extent of each sac was 8 mm., and the width 7·5 mm. The length of the Fish itself was 6 inches.

The tripus occupies its normal position along the side of the complex centrum; its anterior process, which is much the longest, is connected by a short interossicular ligament with the convex outer surface of the scaphium; the articular process is very slender and directed obliquely backwards to an articular pit on the lateral surface of the complex centrum. Unlike most other abnormal Siluridæ, the crescentic process retains its normal shape and curvature. For the terminal part of its course the process is bent downwards in contact with the side of the complex centrum; the root of the process passes through a foramen at the antero-internal extremity of the osseous funnel, and anteriorly to the foramen gives off the articular process from its inner margin, and is then prolonged forwards as the anterior process. The scaphium consists of spatulate and condylar processes only, the ascending process being entirely suppressed. The spatulate process lies at the bottom of a deep notch in the posterior margin of the exoccipital and, as in *Glyptosternum*, projects so much inwards as to lie on the dorsal surface of the basioccipital within the cranial cavity. The intercalarium is a minute nodule of bone imbedded in the interossicular ligament. We could detect no trace of claustra.

The cavum sinus imparis and its atrial diverticula are certainly normal, and we had no difficulty in detecting a tranversely disposed ductus endolymphaticus, but we were unable to arrive at any satisfactory conclusion as to the presence or absence of a sinus endolymphaticus.

From their thinness and partial translucency the lateral and cutaneous areas (fig. 69, *l.c.a.*) are readily noticed in an external view of the Fish. Each area is bounded by, and adherent to, the post-temporal in front, the upper lip of the mouth of the osseous funnel (*t.p.*^{4}) above, and the lower lip of the funnel and the distal extremity of the transverse process of the fifth vertebra below. The lateral line canal (*l.l.c.*), with its protective tubular ossicles, crosses the upper margin of each area.

GROUP :—MALAPTERURINA.

Malapterurus electricus.

G. ST. HILAIRE and JOHANNES MÜLLER have referred to the air-bladder of this species. The former in his work on Egypt (35) gives a brief description of the external appearance of the organ which he also figures (*loc. cit.*, Plate 12, fig. 4), while MÜLLER (28) simply includes *Malapterurus* among those Siluridæ in which he had found an "elastic-spring" apparatus. SÖRENSEN (36) has also figured the air-bladder, and in a recent paper (37) has described the mode of formation of the terminal plates of the "elastic springs." The promise of an anatomical investigation of *Malapterurus* by the late Professor GOODSIR, referred to by MURRAY in his "Remarks on the Natural History of Electric Fishes" (28A), was fulfilled by Dr. CLELAND (6A).

The complex and fifth vertebræ are firmly connected together by investing superficial ossifications, as well as by the partial anchylosis of their neural arches and spines. Their centra are nearly equal in size, that belonging to the complex vertebra being but a trifle the longer of the two. The body of the first vertebra is very feebly developed in the form of a thin, wafer-like bone, wedged in between the basioccipital and complex centrum. In correlation with the absence of a dorsal fin the anterior neural spines are very short, and none are cleft for the support of interspinous bones. The arch and short spine of the third vertebra (fig. 72, *n.s.*^{3}) are inclined forwards towards the supraoccipital and exoccipitals, and connected therewith by a considerable amount of intercalated cartilage. The spine of the fourth vertebra is almost obsolete, and that of the fifth (*n.s.*^{5}) is but feebly developed, serving merely to buttress the much stronger spine of the sixth vertebra. The sixth vertebra itself is quite free, both as regards its centrum, arch, and spine.

Each of the transverse processes of the fourth vertebra is cleft to its root into distinct anterior and posterior divisions (fig. 72). The former (*t.p.*^{4}*a.*) has an extremely thin but highly elastic root, which grows out from the neural arch of the complex vertebra, and at its origin is slightly oblique in a direction from below upwards and backwards. After a slight ventral flexure the elastic root expands at its distal extremity into a very thin, transversely-disposed oval plate of extremely brittle bone, which is closely applied to the outer portion of the anterior wall of the air-bladder rather than to the antero-lateral region, the two surfaces of the plate looking directly forwards and backwards respectively. The posterior face of each plate is faintly concave, the anterior very slightly convex. The protractor muscle of this "elastic-spring" mechanism has an origin and an insertion precisely similar to the corresponding muscle in *Auchenipterus,* and the effect of its contraction will be to pull the oval plate directly forwards towards the inferior limb of the post-temporal. The forward movement of each plate is confined within certain definite and comparatively restricted limits by a projecting process of bone which grows out from the anterior surface of the elastic root and extends towards, but without quite reaching, a facet on the anterior margin of the arch of the complex vertebra, immediately in front of the foramen for the exit of the roots of the fourth spinal nerve (fig. 72, *sp.n.*^{4}). The forward movement of the plate on the contraction of its protractor muscle (*pt.m.*) will soon bring the process and the facet into direct contact, and any further movement in the same direction will be at once checked. The posterior division of the transverse process (*t.p.*^{4}*p.*) is somewhat expanded but not decurved, and its root partially coalesces with the more slender transverse process of the fifth vertebra (*t.p.*^{5}). Both processes have their ventral surfaces adapted to the convex dorsal side of the anterior compartment of the air-bladder. The transverse processes of the sixth vertebra (*t.p.*^{6}) are long and slender, with short ribs (*r.'*) at their distal extremities. It is interesting to remark that, although each of the transverse processes of the fourth vertebra is modified to form an "elastic-spring" mechanism, it differs less from a normal process than is the case with either *Oxydoras* or *Auchenipterus,* and in this respect more closely resembles the only other African Siluroid (*Synodontis*) in which this mechanism is known to exist. Not only does the process retain its characteristic anterior and posterior divisions, but the former more nearly resembles a normal and inelastic anterior division in its relations to the anterior wall of the air-bladder.

Superficial ossifications invest and greatly thicken the sides of the complex and fifth vertebral centra, their free ventral margins forming the lateral boundaries of a well-marked aortic groove. Anteriorly each ossification terminates in a lateral outwardly projecting ridge coincident with the anterior margin of the complex centrum, and at the dorsal extremity of each ridge there is a small but distinct radial nodule suturally attached to the side of the centrum. From each nodule a slender splint-like dorsal lamina passes ventrad to the posterior cardinal vein, and eventually fuses with an oblique outwardly directed ridge on the ventral surface of the posterior division of the transverse process of the fourth vertebra, but for the remainder of its extent the channel for the cardinal vein is a deep groove between the thickened dorsal edge of each superficial ossification and the overlying roots of the transverse processes of the fourth and fifth vertebræ. Posteriorly the superficial ossifications terminate in oblique thickenings, the ventral extremities of which are very similar to accessory articular processes, and overlap the anterior margin of the centrum of the sixth vertebra.

The relatively feeble development of the shoulder-girdle in *Malapterurus*, and the laxity of its connection with the skull, are obviously correlated with the absence of the large pectoral spines which are so characteristic of most other Siluridæ. The post-temporal is but loosely connected with the skull, its ascending process being movably connected with the pterotic and epiotic bones by ligament, while the articulation of the inferior limb with the basioccipital is of a similar character. The clavicular groove is so slight as scarcely to deserve the name of socket, the connection of the clavicle and post-temporal being mainly effected by strong ligamentous fibres.

The air-bladder (fig. 71) consists of two divisions, a relatively small anterior one, which represents a normal bladder, and is divided into an anterior (*a.c.*) and two lateral (*l.c.*) compartments by a primary transverse (*t.s.*) and a longitudinal (*l.s.*) septum; and a somewhat larger posterior sac (*p.c.*), oval in shape, and extending backwards in the abdominal cavity nearly as far as the anus. A contracted tubular portion connects the two divisions, and the longitudinal septum (*l.s.*), which separates the two lateral compartments anteriorly, extends also through the tubular isthmus and the posterior sac, and subdivides the cavity of the latter into a right and left chamber. The posterior sac (*p.c.*) has the shape of a much elongated oval; its walls are moderately thick, but strengthened internally by a number of transversely arranged circular fibrous ridges which project freely into the cavity of each of its chambers. The anterior division of the bladder is somewhat cordate in shape, a deep notch in the median line of its anterior wall partially dividing it into two laterally and forwardly bulging halves. The transverse septum (*t.s.*) is rather narrow, but widens out to some extent before blending with the ventral wall of the bladder. The anterior chamber (*a.c.*) is greatly constricted longitudinally in the median line, first, by the deep notch in its anterior wall, and, secondly, by the unusual prominence of the medio-dorsal ridge which results from the impression of the subvertebral keel; hence it is that the lateral halves of the chamber intercommunicate by a comparatively small aperture. Both the anterior and lateral compartments have relatively thin walls, and the latter exhibit no trace of secondary transverse septa.

In the disposition of the fibres forming the walls of the anterior chamber, and in their relations and attachments to fixed or movable portions of the skeleton, *Malapterurus* differs in no essential feature from *Macrones*. The skeletal insertions of the posterior pillars are shown in fig. 71 (*p.p.*). The dorsal portion of the primary transverse septum (*t.s.*) splits beneath the centrum of the fifth vertebra into two diverging bundles of fibres, which pass dorsally, one on each side of the centrum, and eventually, after curving forwards into the dorsal wall of the anterior chamber, become firmly attached to the lateral surfaces of the complex centrum, to the posterior margins of the dorsal laminæ, and to the prolongations of the latter on to the ventral surfaces of the transverse processes of the fourth vertebra. Unlike *Oxydoras* and *Auchenipterus*, the walls of the anterior chamber are not specially thin where the oval plates of the "elastic-spring" mechanism are applied to them. A transverse membrane, with skeletal attachments in every way similar to those of the corresponding structure in *Auchenipterus*, invests the proper anterior wall of the bladder.

With reference to the mode of growth of the terminal plates of the "elastic-spring" apparatus, Sörensen says (37, p. 140): "Chez le genre *Malapterurus*, le disque mince du ressort n'est pas une ossification de la vessie natatoire (car on peut en suivre la membrane externe le long de sa surface postérieure concave), mais seulement de la plèvre, qui est très épaisse et très ferme en avant, à côté de la partie antérieure de la vessie natatoire." The plates are not, therefore, to be regarded as ossifications of any portion of the tunica externa, but of the transverse membrane only.

The Weberian ossicles require no special description. The scaphium has a long and slender ascending process, in addition to spatulate and condylar processes. The intercalarium is a small nodule of bone in the interossicular ligament. The crescentic process of the tripus curves gradually downwards and inwards from its root towards, and in contact with, the lateral surface of the complex centrum. Claustra are present and occupy their usual position, one on either side of the foramen magnum.

We could detect no deviation from the normal type, either in the structure of the membranous labyrinth of the internal ear, or in the structure and mode of formation of the cavum sinus imparis and atrial cavities.

The dorso-lateral and ventro-lateral muscles of the trunk diverge so slightly that special lateral cutaneous areas can hardly be said to exist.

Malapterurus beninensis.

From Cleland's account (6A) it may be inferred that this species closely resembles *M. electricus*, except that the intercalarium is said to be absent.

Sub-Family :—SILURIDÆ ANOMALOPTERÆ.

Group :—Hypophthalmina.

Hypophthalmus marginatus.

Ramsay Wright (44) has given an account of the air-bladder and anterior vertebræ of this aberrant Siluroid. To admit of comparison with other types, a brief statement of his results may not be out of place, more particularly as *Hypophthalmus* exhibits a remarkably abnormal condition of these structures, and is, moreover, one of the nine genera of Siluridæ in which Johannes Müller denied the existence of an air-bladder.

Complete anchylosis has taken place between the conjoined anterior vertebræ from the first to the fifth inclusive. These vertebræ apparently form a "complex," which represents not only the complex vertebræ of other Siluroids, but the first and fifth as well, and except for a partial intervertebral suture between the fourth and fifth, are indistinguishably fused together. Each of the transverse processes of the fourth vertebra is said by RAMSAY WRIGHT to consist of a dorsal and a ventral* lamina, the former having its origin from the neural arch and the latter from the centrum of the complex vertebra. The two plates approximate and face posteriorly, but remain widely separated anteriorly so as to enclose a cavity between them which is open distally in the dry skeleton, but closed in front by the bones forming the posterior face of the skull, and encloses the rudimentary air-bladder. Not only are the skull and vertebral column firmly anchylosed together, but the three anterior vertebral centra, that is to say, the first and the anterior portion of the complex, and those parts of the Weberian mechanism usually associated with them, including the claustra, scaphia, intercalaria, the anterior portions of the tripodes, the saccus paravertebralis and the atrial cavities, are telescoped, as it were, on to the upper surface of either the basioccipital or exoccipitals, according as they are median or paired lateral structures, and consequently lie altogether within the hinder part of the cranial cavity. The centrum of the first vertebra is situated on the cranial surface of the basioccipital, within the foramen magnum, and on the dorsal surface of the former are placed the two atrial cavities, excavated in the substance of a thick mass of dura mater, and separated from each other by a median partition of the same material. The roof of the cavum sinus imparis is only partially ossified as a thin plate of bone entirely distinct from the exoccipitals. The floor of the cavum is formed by the basioccipital and exoccipitals, but in consequence of the forward dislocation of all the structures concerned the scaphia form its lateral walls, instead of those of the atrial cavities, as is the case with nearly all other Siluroids.

A complete series of Weberian ossicles is present, including the claustra, but no special description of them is given.

The air-bladder is completely divided into two laterally situated air-sacs, each of which lies in the cavity enclosed by the so-called dorsal and ventral laminæ of the corresponding transverse process of the fourth vertebra. Each sac is slightly constricted in the middle, and while the outer half is membranous, the inner is ossified in such a way as to form a bony cup, which is continuous at its outwardly directed free margins with the membranous portion, but at its closed base is confluent with the arch and centrum of the complex vertebra. The osseous half of the bladder is evidently the result of the ossification of the tunica externa, and its subsequent fusion with the wall of the neural canal. Internally the entire bladder is lined with tunica interna. A connection between the hinder end of the tripus and the membranous portion of the bladder could still be traced. No communication between the two air-sacs, or between the latter and the œsophagus, was discovered.

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* We have elsewhere given reasons for the belief that the so-called ventral lamina is really no part of the transverse process, but ought rather to be regarded as the equivalent of the ventral process of *Bagarius*, and, like the latter, probably owes its formation to the extension of ossified deposit from the superficial ossifications of the complex centrum into the ventral portion of the superficial coat of the air-bladder. (See Morphological Summary, p. 224).

Although RAMSAY WRIGHT mentions and figures a transverse ductus endolymphaticus (*loc. cit.*, Plate 9, fig. 10), no reference is made to the presence or absence of a sinus endolymphaticus, and in none of his figures of sections taken through the cavum sinus imparis is that structure represented as present. It would certainly be interesting to know definitely if the omission is really due to the absence of the sinus, for if such be the case *Hypophthalmus* must be included with *Bagarius* and *Glyptosternum* as an additional example of the correlation of retrogressive changes in the air-bladder with degeneration of that portion of the internal ear which is physiologically related to the bladder through the Weberian mechanism.

SUB-FAMILY :—**SILURIDÆ PROTEROPODES.**

GROUP :—HYPOSTOMATINA.

The only examples of this singular group that we have been able to examine were two badly preserved specimens of *Loricaria cataphracta* and *Plecostomus verres*, and a skeleton of *Callichthys littoralis*. We are therefore only able to confirm the general accuracy of REISSNER's statements with reference to these genera and to supplement his results on one or two more or less important points. With these exceptions the only other Hypostomatous Siluroid about which anything is precisely known as to the condition of the air-bladder is *Rhinelepis*.

Acanthicus hystrix.*

For our knowledge of the air-bladder of this Siluroid we are indebted to REISSNER's valuable paper (32). The nomenclature adopted by REISSNER is somewhat difficult to follow, and in giving a brief abstract of his paper we shall attempt to correlate the terms employed by him with those used by us so as to facilitate the comparison of *Acanthicus* with other abnormal Siluroids.

Two egg-shaped, thin-walled, osseous capsules are found one on each side of, and confluent with, the "first" and "second" vertebræ.† Each capsule is somewhat broader in front than behind, with a maximum width of 18 mm. and a length of 32 mm. The two capsules occupy the entire width of the anterior portion of the abdominal cavity, and to a large extent superiorly they are invested by, and anchylosed to, the bones which form the posterior part of the cranial shield. The outer and anterior aspect of each capsule is prolonged downwards as a "processus auricularis,"* while the ventral surface a little behind the middle of the capsule is traversed by a deep transverse groove in which the first rib lies. Posteriorly the two capsules are somewhat contracted and terminate in widely separated free extremities. Certain apertures perforate the walls of each capsule. The ventral surface of the anterior and broader portion is fenestrated by several variously sized foramina. A small oval foramen, the "apertura capsulæ osseæ interna inferior," perforates the antero-internal inferior wall. A larger foramen, the ap. cap. oss. externa, traverses the anterior portion of the outer wall immediately below the postero-lateral cranial plates.† One or two channels also perforate the "processus auricularis," and, like all the preceding ones, communicate with the interior of the osseous capsule. From the apertura capsulæ osseæ interna inferior a slight groove extends on to the internal surface of the inner wall of the capsule in a direction upwards and forwards and finally terminates in an "apertura capsulæ osseæ interna superior"‡ through which the interior of the capsule communicates by means of a cavity in the anterior portion of the "first" vertebra with the hinder part of the cranial cavity. From the inner margin of each ap. cap. oss. int. inf. a very delicate process of bone arises, which curves downwards and inwards and meets its fellow of the opposite side, thus forming a slender arch of bone. A somewhat stouter median spicule descends from the ventral surface of the body of the "first" vertebra and fuses with the apex of the arch formed by the two lateral processes. To this peculiar double arch depending from the under surface of the "first" vertebra REISSNER gives the name of "processus bijugus."

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* *Rhinelepis acanthicus*, CUV. and VAL.

† According to REISSNER the "second" vertebra carries the first pair of ribs. If these structures are really ribs, the vertebra is either the fifth or the sixth, but if they are merely transverse processes it is probably the fifth. The "first" vertebra is, therefore, a "complex," and includes the first to the fourth vertebræ inclusive, with the possible addition of the fifth.

The air-bladder is constricted into two laterally situated oval air-sacs which occupy the cavities of the two osseous capsules. The walls of the sacs are everywhere in close contact with the inner surfaces of their investing capsules, but are only attached thereto by a few fibres which are said to transmit blood-vessels and possibly nerves. Although no connection between the two sacs could with certainty be determined REISSNER regards it as extremely probable that such communication does exist, and believes that the tubular connecting duct is supported by the "processus bijugus," § and opens into each air-sac through the "apertura capsulæ osseæ interna inferior."‖

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* From the analogy of *Cobitis* REISSNER thinks that this process may represent the distal end of a transverse process; if this be so, it must belong to the fourth vertebra, but much more probably, however, it is the post-temporal.

† This may correspond to the distal aperture of the funnel-shaped transverse process in other abnormal Siluridæ, or possibly to a very similar aperture which is found in each of the outer walls of the osseous capsules of the Cyprinoid *Cobitis* and its allies.

‡ An equivalent to this aperture is found in other Siluroids (*e.g.*, *Callomystax*) at the antero-internal angle of each bony capsule, where there is a foramen through which the tripus passes to its connection with the scaphium anteriorly.

§ From the analogy of *Plecostomus* we have no doubt that REISSNER's belief is correct.

‖ There is one point in connection with the air-bladder in which *Acanthicus* is unique among the Siluridæ. REISSNER describes the first pair of ribs as occupying well marked grooves on the ventral

A tripus and a scaphium are described by REISSNER but no mention is made of claustra or intercalaria. The scaphium is a small concavo-convex ossicle without ascending or condylar processes. The tripus has a straight posterior process in addition to the usual anterior and articular processes. For the greater part of its extent each tripus is said to occupy the cavity in the first vertebra through which, according to REISSNER, the cranial cavity communicates with the interior of the osseous capsule. The posterior process of the ossicle, after traversing the "apertura capsulæ osseæ interna superior," gains the interior of the capsule and becomes connected with the air-sac.

The relations of the sinus endolymphaticus and atrial cavities are carefully described The sacculi are said to lie in two shallow depressions, separated by a slight median ridge on the dorsal surface of the os basilare (basioccipital), in this respect resembling several of the Loricaroid genera, and to be connected by a transverse ductus endolymphaticus. In the absence of figures we are not quite clear as to the exact relations of the sinus endolymphaticus and the atria to the anterior vertebræ and cranial cavity, but as far as we can make out from REISSNER's description they appear to occupy a Y-shaped groove on the dorsal surface of the basioccipital and the anterior portion of the body of the "first" vertebra, the stem of the Y, which is directed forwards indicating the position of the cavum sinus imparis and the enclosed sinus, while the backwardly and outwardly extending arms indicate the position of the two atrial cavities. In any case we infer that the cavum, like the atria, has only a fibrous roof, and this is apparently also true of the depressions for the sacculi, unless indeed, the latter are freely exposed in the floor of the cranial cavity. The want of the usual bony roof to these cavities or recesses may possibly be due, as we would suggest, to the failure of the exoccipitals to develop their usual horizontal plate-like ingrowths.

Loricaria cataphracta and *L. nudirostris.*

Two ill-preserved examples of these species were also examined by REISSNER (32), and, in all essential points affecting the structures under consideration, were found to be in close agreement.

The "first" vertebra is said to be connected with the second by a strongly-toothed suture, and the neural arches of both to possess large "processus spinosi superiores," united by a serrated suture with the "os occipitale superius" (supraoccipital) in the median line. The "first" vertebra is provided with two peculiarly-shaped lateral processes, which REISSNER regards as probably corresponding to modified "processus transversi." Each process is slightly curved in a direction outwards and backwards, and at its proximal extremity encloses a spherical cavity. Externally this cavity

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surfaces of the bony capsules. It will follow, therefore, that rather more than a third of the length of the capsules and their enclosed air-sacs must be *dorsad* to the ribs, instead of ventrad to them, and probably project backwards above the ribs into the dorso-lateral muscles.

becomes a deep groove, which is open in front, at all events so far as the transverse process itself is concerned, and gradually dies away towards the distal end of the process. The groove is not an open one, inasmuch as its superior margin joins the inferior edge of the "os occipitale externum" (post-temporal) and its inferior margin the posterior edge of the same bone, so that the groove becomes a closed canal, except that it has a distal aperture between the free edge of the transverse process and the overlapping "os occipitale externum." Near the distal aperture of the canal there is a small area of soft skin, between the cranial plates and those which invest the lateral surface of the trunk.

The cavity enclosed by the proximal portion of the transverse process is separated from the outer groove by a slight ridge, and contains a globose membranous bladder, which, from the analogy of *Acanthicus*, REISSNER rightly regards as equivalent to one-half of the air-bladder. From the inner wall of the cavity of the transverse process a narrow canal extends inwards and forwards, and in this canal lies the almost rectangularly bent tripus.* This ossicle is said to consist of two processes united at a right angle, and of these one is transversely disposed and connected with the wall of the corresponding air-sac, while the other, or anterior process, projects from the canal in which it is lodged into the cranial cavity, a scaphium similar to that of *Acanthicus* being attached to its free extremity. A membranous canal is said to leave each air-sac and to pass through the hinder wall of the cavity of the transverse process, *probably* for the purpose of effecting a communication with the sac of the opposite side. A perfect "processus bijugus" could not be found, but two osseous processes on the inferior surface of the "first" vertebra, and a slender, bony spicule which is directed inwards and backwards from near the root of each transverse process may possibly represent this structure. Possibly, REISSNER remarks, the spicules, or tendinous prolongations therefrom, may be continuous with the two bony processes.

No reference is made to the internal ear or to the cavum sinus imparis and its atrial cavities.

We are able to supplement REISSNER'S somewhat imperfect description with a few additional particulars.

The "second" vertebra of REISSNER is probably the fifth, and hence, his "first" vertebra really represents the complex vertebra of other Siluroids (see RAMSAY WRIGHT, 44, p. 109). The centrum of the true first vertebra is either wanting, or has fused with the complex, but in the latter case no intervertebral suture could be detected. The posterior face of the complex centrum has a deep tubular concavity, but the almost flat anterior face articulates with the contiguous surface of the basioccipital by an interdigitating suture. Almost complete fusion, however, has taken place between the arch and spine of the complex vertebra and the supra- and exoccipitals, but from the position of the external atrial apertures, and the mode of articulation of the complex vertebra with the basioccipital, it is clear that nothing comparable to the singular forward dislocation of the anterior vertebræ through the foramen magnum and into the cranial cavity, which is so remarkable a feature in *Hypophthalmus*, takes place in *Loricaria*. The bony capsules for the air-bladder are formed by the transverse process of the fourth vertebra in conjunction with certain of the bones forming the posterior face of the skull, viz., the posterior plates of the exoccipitals, the epiotics, and possibly the pterotics, in much the same fashion as in *Hypophthalmus*, except that the post-temporals form the external walls of the capsules and more or less completely close their terminal apertures.

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* This canal is really a simple aperture between the exoccipital and the arch of the complex vertebra, and corresponds to that portion of the wall of the neural canal which in other Siluroids is fibrous.

As in *Acanthicus* the sacculi occupy shallow depressions in the cranial surface of the basioccipital, separated by a faint median ridge. It is possible that these structures may have a fibrous roof, but it is certain that they are not invested dorsally by horizontally disposed bony plates derived from the two exoccipitals. We could not with certainty localize the position of the cavum sinus imparis and its atria, but they are probably situated on the dorsal surface of the basioccipital, between the depressions for the sacculi anteriorly, and the apertures whereby the anterior extremities of the tripodes enter the neural canal posteriorly. In that position, and as in *Acanthicus*, there is a slight median depression, which divides behind into two short inconspicuous grooves leading towards the apertures in question, and may possibly indicate the position of these cavities, but if such be the case their walls must be largely fibrous. The scaphia and the anterior extremities of the tripodes project freely into the occipital portion of the cranial cavity, and from the position of the former ossicles it is clear that the external atrial apertures must also be within the cranial cavity, as is the case with such other abnormal Siluridæ as, for example, *Callomystax*. The condition of our specimen was fatal to a satisfactory examination of the internal ear. We were able to ascertain that a very short ductus endolymphaticus is present, but whether a sinus endolymphaticus is present or absent we cannot with certainty say.

The air-bladder has extremely thin but structurally perfect walls. Each lateral air-sac is confined to the more dilated proximal portion of its bony capsule, which, as REISSNER states, is separated from the distal portion by a slight transverse ridge.* Apart from their connection with the tripodes, which appears to be perfectly normal, the walls of the air-sacs are free from any special attachments to the skeleton or to the inner surfaces of their bony capsules. There is no doubt as to the existence of a connection between the two sacs by means of an extremely slender, thin-walled intermediate canal, which leaves each capsule at the point indicated by REISSNER.

The articular process of the tripus is situated at the point of junction of the anterior and posterior processes, which, as REISSNER states, are united at a right angle. Neither claustra nor intercalaria could be detected.

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* In our specimen each sac was about 8 mm. in length and in width, the length of the Fish being 7 inches.

Hypostomus verres, Cuv. and Val. (= *Plecostomus verres*?)

According to Reissner (32) this species agrees in all important details with *Loricaria*, but has a more perfectly formed "processus bijugus."

These statements we are able to confirm. In the condition of its anterior vertebræ and in the mode of formation of the osseous capsules for the two air-sacs, as well as in the absence of a bony roof to the recess for the sacculi and the cavum sinus imparis, *Plecostomus* closely agrees with *Loricaria*.

We have satisfied ourselves that the "processus bijugus" in *Plecostomus* supports the slender intermediate canal by which the two air-sacs are placed in communication with each other. In this respect *Plecostomus* confirms Reissner's suggestions as to the object of this singular structure in *Acanthicus*.

We could detect no trace of either intercalaria or claustra.

Callichthys asper.

Of this species Reissner (32) remarks that he had only a very small and badly preserved specimen for examination. In the structure of the cranium and the condition of the "first" vertebra, the air-bladder and Weberian ossicles this Siluroid is said to be more closely allied to *Plecostomus* than the latter is to *Loricaria*. The "processus bijugus" is said to be similar to that of *Plecostomus*, and in connection with its arch Reissner found a minute canal which, he adds, probably served the purpose of uniting the two divisions of the air-bladder. The tripus is slightly bent, and divides anteriorly into two processes, one for attachment (articular process), and the other for connection with the deeply concave scaphium.

As far as we were able to determine from the external examination of a Museum skeleton of *Callichthys littoralis*, this species closely resembles *Loricaria* in the modifications which the anterior vertebræ undergo, and in the mode of formation of the osseous capsules for the air-bladder, but the union of the vertebral column with the skull seems to be more intimate than in either *Loricaria* or *Plecostomus* (*Hypostomus*).

Sisor.

Without reference to any particular species, Day (9) thus refers to the condition of the air-bladder in this genus:—"Subvertebral bony capsules were present, and apparently contained an air-vessel, whilst none could be detected in the abdomen."

Pseudecheneis.

Of this genus the same observer (9) remarks that the air-vessel is "in two rounded lateral portions, and enclosed in bony capsules."

Exostoma Blythii, DAY.

Of this Siluroid, DAY (9) says :—"Air-vessel in a globular form, on either side of the body of the anterior vertebræ, and enclosed in bone."

GROUP :—ASPRĖDININA.

Aspredo cotylophorus.

This South American genus is regarded by COPE (7) as the type of a distinct family (Aspredinidæ) of the order Nematognathi (= Siluridæ). The only reference to the air-bladder of *Aspredo* that we are acquainted with is by CUVIER and VALENCIENNES in their 'Histoire Naturelle des Poissons,' vol. 15, 1840. The air-bladder of "*Aspredo lævis*" (= *A. batrachus*) is there briefly described as composed of two ovoid lobes with fibrous walls of a silvery lustre.

In *Aspredo cotylophorus* the skull, with the first, the complex, and the fifth vertebræ, are immovably connected together. The body of the first vertebra (figs. 73, 74, *v.*^{1}) is fairly well-developed, though somewhat smaller than the normal centra, and so obliquely placed, that its anterior and posterior concavities are directed forwards and downwards and backwards and upwards respectively (fig. 74). The complex centrum (figs. 73, 74, *c.c.*) is unusually long and narrow, and is, moreover, so bent upon itself that while its deep and almost tubular posterior concavity looks directly backwards, its cup-shaped anterior face is directed downwards as well as forwards to meet the upturned posterior face of the centrum of the first vertebra (fig. 74). The centrum of the fifth vertebra (*v.*^{5}) is almost as long, and its deep tubular anterior concavity is in striking contrast to the relatively shallow posterior concavity. The sixth vertebra (fig. 73, *v.*^{6}) is quite free and distinct from the foregoing; its short transverse processes carry the first pair of ribs.

The neural arches of the complex and fifth vertebræ (fig. 74) are almost completely confluent. The coalesced spinous processes of the third and fourth vertebræ (figs. 74, 75, *n.s.*^{3}, *n.s.*^{4}) are represented by a low, compressed ridge of bone of uniform height, but greatly thickened along its free dorsal margin. The anterior edge of the ridge, with the neural arch of the third vertebra, incline forwards to a firm sutural union with the supraöccipital and exöccipitals, while the posterior margin considerably overlaps, and partially coalesces with, the spine of the fifth vertebra. The latter (*n.s.*^{5}) is very strongly developed, inclined obliquely backwards, and cleft for the support of the anterior interspinous bones.

The transverse processes of the fourth and fifth vertebræ (figs. 73 to 75, *t.p.*^{4}, *t.p.*^{5}) combine to form on each side a narrow wing-like outgrowth, which is much longer than broad, slightly concave from before backwards on its ventral surface, and has its anterior and posterior margins strongly thickened and produced distally into free projecting processes (fig. 73). The transverse process of the fourth vertebra (*t.p.*^{4}) consists of a thickened anterior part which curves downwards, and for a portion of its extent has its anterior face closely applied to the inferior limb of the post-temporal, while its free distal extremity furnishes a posterior wall to the socket for the clavicle. The remainder of the process is a thin narrow lamina of bone, curving at first upwards and backwards, and then slightly downwards to meet a somewhat similar but shorter lamina, derived from the anterior margin of the transverse process of the fifth vertebra. The latter (*t.p.*^{5}), in addition to the lamina already mentioned, consists of a long stout process, which has its free projecting extremity connected by a ligament (fig. 73, *lgt.*) with the larger of the two processes, into which the proximal end of the clavicle divides.

Superficial ossifications thicken the lateral surfaces of the complex and fifth vertebral centra, but are interrupted intervertebrally by an irregular interdigitating suture. Their dorsal and ventral edges respectively form the inferior lips of cardinal grooves, and the lateral margins of a median aortic groove (fig. 73). Small radial nodules are suturally attached to the sides of the complex centrum, and a slender spicular dorsal lamina (*d.l.*), with the usual relations to the corresponding cardinal groove, is prolonged from each nodule and blends with the ventral surface of the transverse process of the fourth vertebra.

The post-temporal has the usual three divisions. The slender inferior limb (fig. 73, *pt.i.*) is largely supported by the thickened and decurved anterior portion of the transverse process of the fourth vertebra. Between the inferior limb and the stem of the bone there is a deep groove, which is closed behind by the transverse process, and converted into a tubular socket for the head of the clavicle. The posterior margin of the stem (fig. 75, *pt.s.*) is coincident with, and closely applied to, the similarly curved distal extremity of the same transverse process. The ascending process (*pt.a*) is very slender, articulating above with the supraoccipital and epiotic, and nearly meeting the pterotic in front. The proximal end of the clavicle is divided into two processes, a slender peg-like process for insertion into the clavicular socket, and a strong triangular outgrowth (*cl'.*) which is directed backwards dorsad to the origin of the pectoral fin, and takes the place of the proper posterior process (*cl.p.*) in forming the inferior limit of the contiguous lateral cutaneous area. A strong ligament (fig. 73, *lgt.*) connects the distal extremity of the process with the transverse process of the fifth vertebra.

In consequence of the peculiar flattened condition of the head and the adjacent portion of the trunk in this genus, the extensive lateral cutaneous areas (fig. 73, *l.c.a.*) are situated rather on the dorsal than the lateral surfaces of the body. Each area is peripherally attached to the curved distal margins of the modified transverse processes of the fourth and fifth vertebræ above, in front to the posterior margin of the stem of the post-temporal, and inferiorly, or rather externally, to the clavicular process and to the ligament leading therefrom to the transverse process of the fifth vertebra.

The true posterior process of the clavicle (fig. 75, *cl.p.*), instead of marking the inferior boundary of a lateral cutaneous area, is directed backwards on the ventral side of the body and related solely to the insertion of the ventro-lateral muscles of the body-wall.

The air-bladder (fig. 76, *a.b.*) is partially constricted into two laterally situated and somewhat ovoid or globose sacs by deep emarginations in its anterior and posterior walls.* Each half of the bladder occupies the shallow bony recess formed by the modified transverse processes of its side. Nearly the whole extent of the lateral or outer wall of each sac, as well as a part of the dorsal wall, are in close contact with the inner surface of a lateral cutaneous area. The opening of the ductus pneumaticus (*d.p.*) is in the medio-ventral line, but nearer to the anterior than the posterior end of the bladder. On removing the ventral wall (fig. 77) it at once becomes obvious that the lateral portions of the organ are in free and open communication with each other, and further, that by far the larger portion of the bladder corresponds to the anterior chamber only of the normally developed structure. A very narrow transverse septum (*t.s.*) is present, but situated so near to the posterior wall that there exists but the barest vestige of a longitudinal septum (*l.s.*), and if lateral compartments can be said to be represented at all it can only be by the postero-internal portions of the lateral halves of the bladder.

In the general structure of the walls of the bladder, which it may be mentioned are extremely thin, and in the nature and extent of its various skeletal attachments, *Aspredo* differs in no essential feature from *Macrones.* The transverse septum is attached dorsally to the ventral surface and sides of the body of the fifth vertebra, and anteriorly and laterally to this to the posterior margins of the dorsal laminæ. The anterior pillars are inserted by their dorsal edges into the radial nodules, as well as to the lateral and ventral surfaces of the anterior portion of the complex centrum, and the fibres of the two strata of the tunica externa in converging from the antero-lateral and lateral walls to their attachments to the crescentic processes of the tripodes (*tr.c.*) form the usual well-defined triangular sheets (fig. 77).

The tripus (figs. 73, 77, *tr.*, *tr.c.*) has a short inwardly-curved crescentic process, and a relatively long anterior process. The intercalarium is a very small nodule in the interossicular ligament. The scaphium has no ascending process, but is otherwise complete. The claustra are extremely small spicular ossicles in the usual position.

The recesses for the sacculi are unusually shallow, and the cavum sinus imparis is relatively shorter than in most other Siluridæ. The atrial cavities are normal, except that their external apertures and the scaphia which close them, as well as the interossicular ligament, lie altogether within the neural canal on the dorsal surface of the centrum of the first vertebra. We observed no indications of degeneration in the structure of the internal ear.

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* The width of the bladder in our specimen was 17 mm., and the length of each half 10 mm. The length of the Fish was 6 inches.

At first sight it would seem that, so far as its air-bladder is concerned, *Aspredo*, while more closely resembling the normal Siluridæ than any of the truly abnormal species that we have yet described, nevertheless presents an interesting connecting link between the two extremes. At any rate, this conclusion is suggested by the almost complete suppression of lateral chambers, and the partial constriction of the organ into two laterally situated air-sacs. On the other hand, the air-bladder is by no means small in proportion to the bulk of the Fish; and bearing in mind, also, that there are no obvious indications of retrogression, either in the Weberian ossicles themselves or their connection with the bladder, or in the condition of the internal ear, it seems reasonable to suppose that all these structures are as truly functional as in those species with more typical bladders. It may, therefore, be suggested that such an apparently retrogressive feature in the air-bladder of *Aspredo* as the practical atrophy of the lateral chambers is really related to the peculiarly flattened and shortened condition of the body, and is not to be taken as conclusive evidence of degeneration. At the same time, we admit that the atrophy of the lateral chambers must render the air-bladder and the Weberian mechanism less sensitive as a register of varying hydrostatic pressures.*

SUB-FAMILY:—**SILURIDÆ HOMALOPTERÆ.**

GROUP:—CLARIINA.

Clarias nieuhofii.

TAYLOR (38) has given a brief description of the air-bladder of *Clarias magur* (under the name of *Macropteronotus magur*) to the following effect:—The bladder consists of two small pyriform sacs joined at their pointed extremities by an intermediate canal. The organ is said to lie across the spine, and each of its two pyriform portions to be contained in a funnel-shaped case projecting outwards from the side of the body of the "first" vertebra, and having its mouth covered over by the common integument, as in "*Pimelodus bagharia*" (= *Bagarius Yarrellii*). The case is formed of bone, but above and below by a tendinous membrane that extends across the inferior surface of the first vertebra, thus protecting from pressure the intermediate canal or isthmus by which the two pyriform sacs are united. A communication exists between the air-bladder and alimentary canal by a small ductus pneumaticus passing from the intermediate canal to the œsophagus.

CUVIER and VALENCIENNES (8) refer to a species of this genus under the name of *Clarias hasselquistii* in which the air-bladder is described as being small and formed of two rounded lobes, almost entirely separated the one from the other, and sunk in great hollows situated in front of the "apophysis of the large vertebra." These lobes are said to communicate under the body of the vertebra, but from the fact that the bladder had already been displaced, the writer adds that he was not certain how it was attached, and that the ligaments deserve a new and special dissection.

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* See Physiological section.

DAY (9) also briefly refers to the air-bladder of *Clarias*, and includes the genus in his list of Siluridæ in which the organ is said to be constricted into two lateral portions, and more or less completely enclosed within bony capsules.

Our own investigations have been confined to *Clarias nieuhofii*, *C. magur*, *C. fuscus*, and *C. anguillaris*.

In *Clarias nieuhofii* the skull and the first, the complex, and the fifth vertebræ are rigidly connected together (i.) by the superficial ossifications which continuously invest the lateral surfaces of the various centra, and also extend on to and thicken the sides and under surface of the basioccipital; and (ii.) through the firm sutural union of the correlated vertebral and cranial elements (figs. 78, 79). The body of the first vertebra (fig. 79, $v.^1$) is very small; its dorsal surface forms part of the floor of the neural canal, but the ventral and lateral surfaces are covered by the forward extension of the superficial ossifications on to the basioccipital (*b.o.*). In a vertical longitudinal section of this region of the vertebral column the centrum in question appears as if completely enclosed within the contiguous concavities of the complex centrum and basioccipital. The centrum of the complex vertebra (figs. 78, 79, *c.c.*) is nearly three times the length of that of the fifth, and a single pair of fairly large nutrient foramina are visible on its ventral surface. Except for the asymmetrical development of its concavities, the anterior being much deeper than the posterior, the body of the fifth vertebra ($v.^5$) in no way differs from the normal centra. The sixth vertebra is normal and free (fig. 80, $v.^6$), but, unlike most other Siluridæ, its well-developed transverse processes do not carry ribs, the seventh ($v.^7$) being the first of the rib-bearing series.

The confluent spinous processes of the third and fourth vertebræ (fig. 79, $n.s.^3$), $n.s.^4$), form a thin vertical plate of bone which is much higher behind than in front. The low, but much-thickened anterior margin of the plate, and the neural arch of the complex vertebra incline forwards, so as to abut against the supraoccipital and exoccipitals, a small amount of intercalated cartilage, however, still persisting between the apposed elements. A thin lamina of bone derived from the under surface of the supraoccipital spine (*so.'*) firmly articulates by an interdigitating suture with the dorsal margin of the confluent spines. The uncleft spine and arch of the fifth vertebra ($n.s.^5$) are firmly, but by suture only, united to those of the preceding vertebra. As in nearly all other Siluroid Fishes, the walls of the neural canal are fibrous over a somewhat triangular area (*at.a.*) on each side between the arch of the complex vertebra and the exoccipital (fig. 79).

The transverse processes of the fourth and fifth vertebræ are greatly expanded and so modified as to form on each side a more or less complete bony funnel, which is contracted proximally and expanded distally, and has its long axis disposed at right angles to the axis of the body (fig. 78). Except at its root, which is nearly flat, the transverse process of the fourth vertebra (*t.p.*^{4}) has the anterior margin curved downwards towards the ventral surface, and of this decurved portion the mesial part is prolonged backwards as a somewhat triangular lamina of bone to form a partial floor for the osseous funnel. Near the flat root of the process the decurved anterior margin abruptly ceases, and leaves a cleft between its free inner edge and the lateral surface of the complex centrum, through which the tripus passes backwards from its connection with the scaphium to gain the interior of the funnel. The posterior margin of the process is but slightly decurved except at its outer extremity, where a slender process of bone curves downwards, and forms the posterior lip of the distal aperture of the funnel. The transverse process of the fifth vertebra (*t.p.*^{5}) is comparatively slender, with a flat root and an anterior margin which is suturally united to the posterior edge of the preceding process in the roof of the bony funnel. The distal half of the process, however, has its hinder margin bent downwards and also a little forwards, to meet the recurved anterior edge of the preceding transverse process in the floor of the funnel, and finally ends in a somewhat irregular indentated edge. In this way the transverse process of the fourth vertebra furnishes the anterior and dorsal walls of the funnel and a partial floor, and, in addition, the posterior lip of its terminal aperture, while the corresponding process of the fifth vertebra forms the incomplete posterior wall. So far as the transverse processes are concerned, the bony walls of each funnel are incomplete, both proximally and distally, on the ventral and posterior surfaces; proximally, however, the floor is to some extent completed by a thin, flattened, and tapering process of bone (*v.p.*), which grows out from each of the two lateral ridges bounding the median aortic groove in the region of the complex centrum, and extends outwards to the point where the recurved margins of the two transverse processes nearly meet in the floor of the funnel. This process is clearly the greatly enlarged representative of the ventral process of *Bagarius* and *Glyptosternum*, to which attention has already been directed. Immediately behind the origin of these processes the two lateral aortic ridges are deeply emarginate, to admit of the passage of the median and tubular portion of the air-bladder across the ventral surface of the complex centrum from one lateral air-sac to the other. The anterior margin of the flat root of the transverse process of the fourth vertebra may be traced forwards along the external surface of the neural arch of the complex vertebra in the form of a longitudinal ridge, which finally ceases near the upper lip of the external atrial aperture. A somewhat similar, but more extensive, ridge (*l.r.*), apparently a local thickening of the superficial ossifications of the complex centrum, may also be traced from the lower lip of the atrial aperture obliquely backwards and upwards along the side of the centrum, where it is situated ventrad to the previous ridge, and then curves outwards across the ventral surface of the root of the transverse process of the fourth vertebra, ultimately dying away along the line of junction of the latter with the transverse process of the fifth vertebra in the roof of the bony funnel. As the two ridges traverse each side of the complex vertebra they enclose between them a well-marked groove, the anterior end of which coincides with the position of the external atrial aperture, while the posterior extremity opens into the proximal portion of the cavity of the funnel; this groove lodges the anterior portion of the tripus (*tr.*), and, at about the middle of its extent, deepens into a pit on the side of the complex centrum for the reception of the articular process of the same ossicle. It may be remarked that the groove is almost an exact repetition of the one already described in *Bagarius Yarrellii*, both as regards its mode of formation and contents, while the ridge, which forms its ventral boundary, we identify in each case as the equivalent of the oblique lateral ridge of the complex centrum in the more normal Siluridæ.

Superficial ossifications thicken the sides, and more especially the ventro-lateral margins of the complex and fifth vertebral centra, and also form the lateral boundaries of a median aortic groove; in addition, they invest the lateral and ventral surfaces of the body of the first vertebra and the basioccipital, including the junction of the former with the complex centrum, so that the first intervertebral suture, which is visible on the ventral surface, is the one between the complex and fifth centra (fig. 78). The dorsal lamina of other Siluridæ is represented in *Clarias* by a thin and somewhat flexible process of bone (*d.l.*) which appears to become detached from the oblique lateral ridge of the complex centrum (*l.r.*) at the point where the latter passes on to the ventral surface of the transverse process of the fourth vertebra, and from thence extends obliquely downwards, inwards, and a little forwards towards, but without quite reaching, the lateral surface of the complex centrum, eventually terminating in a thickened and somewhat hook-shaped free extremity (*r.n*). Traced outwards from its nodular free extremity along the roof of the funnel the dorsal lamina becomes confluent with the oblique lateral ridge, but may, nevertheless, be traced as a faint flattened projection, with a ridge-like posterior margin, extending along the hinder edge of the transverse process of the fourth vertebra as far as its distal extremity. There can be no doubt that the hook-shaped extremity of the lamina (*r.n.*) corresponds to the radial nodule of other Siluridæ, inasmuch as it receives the insertion of the radial fibres of the tripus (fig. 81), but, instead of being firmly adherent to the side of the complex centrum, the nodule has become detached therefrom and fused with the inner or free extremity of the dorsal lamina. The anterior extremity of the mesonephros passes forwards between the free portion of each dorsal lamina and the complex centrum, across the flat roots of the modified transverse processes, and the posterior cardinal vein takes a precisely similar course on its way to join the Cuvierian duct of its side. Such other local developments of the superficial ossifications as the oblique lateral ridges of the complex centrum and the ventral processes have been already described.

In the arrangement of the foramina for the exit of the anterior spinal nerves from the neural canal, as well as in the peripheral distribution of the nerves themselves, *Clarias* agrees very closely with *Macrones* (fig. 79).

The post-temporal has only a vestige of an inferior limb (fig. 78, *pt.i.*) which is firmly applied to the distal portion of the anterior wall of the bony funnel of its side, but remains widely separated from the basioccipital (*b.o.*). The expanded stem of the bone (*pt.s.*) is directly continuous with the ascending process (*pt.a.*), and is also traversed on its inner surface by a groove (*cl.s.*) for articulation with the proximal extremity of the clavicle. A backwardly projecting process from the stem (*pt.s.*) is closely applied to the distal extremity of the transverse process of the fourth vertebra in such a way as to encircle the anterior and dorsal lips of the distal aperture of the funnel, the dorsal wall of which is also slightly lengthened, but without in any way closing or diminishing the size of the terminal aperture. Between this process and the outer margin of the roof of the funnel there is a foramen for the transmission of the lateral-line branch of the tenth cranial nerve as it passes backwards from the skull after traversing the dorsal surface of the funnel (*x'.*).

The cavum sinus imparis (fig. 79, *c.s.i.*), the foveæ sacculi (*f.s.*), and the atrial cavities and their external apertures (*at.a.*) differ in no essential feature, either as regards mode of formation, relative size, or mutual relations, from the corresponding structures in *Macrones*, or any other normal Siluroid.

Before dealing with the structure of the air-bladder brief reference may be made to certain investing membranes and other structures which are closely related to its osseous capsules.

As originally stated by TAYLOR (*loc. cit.*), a thin but tough fibrous membrane completes the walls of the bony funnels wherever vacuities exist between the modified transverse processes, or where they are otherwise incomplete, but is apparently restricted to the anterior ventral and posterior surfaces of the funnels. Mesially, the membrane extends across the ventral surface of the complex centrum and there furnishes a tubular investment to the contracted median portion of the air-bladder; anteriorly, it is continuous with the walls of the saccus paravertebralis (fig. 78, *s.pv.*), and apparently also, after extending forwards over the dorsal surface of the bilobed anterior extremity of the mesonephros, with the aponeurotic membrane separating the abdominal cavity from the pericardial and branchial cavities; laterally the membrane extends over and closes the terminal apertures of the two funnels. The precise nature of this investing membrane is difficult to determine. It may be merely a backward prolongation of the aponeurotic membrane over the funnels, or, as is perhaps more probable, the membrane represents what we have elsewhere regarded as the superficial fibrous coat of the air-bladder, and is indicated in the more normal Siluroids by the transverse membrane, or, in certain abnormal forms, *e.g.*, *Bagarius* and *Glyptosternum*, by an external fibrous investment to the ventral surface of the rudimentary bladder. Whatever may be its nature it is highly probable that the walls of the bony funnels are largely formed by the partial ossification of this membrane, either through an invasion of ossified deposit extending from originally more normal transverse processes, or, as in the case of the ventral processes, by the ossification of the ventral portion of the membrane in continuity with the superficial ossifications of the complex centrum.

The bilobed anterior division of the mesonephros occupies a recess of corresponding shape, immediately in front of the two funnels, to the anterior wall of which, and to their investing membrane the gland is closely applied.

The peritoneum covers the ventral surface of the mesonephros, and, anteriorly, is continued over the under surfaces of the funnels. Although elsewhere easily separable from the latter, the peritoneum is firmly adherent to the fibrous portion of their walls, along the horizontal median line of their ventral surfaces, or, more correctly, along the interspace between the recurved margins of the transverse processes of the fourth and fifth vertebræ. This attachment seems exactly to correspond to a similar connection between the ventral edge of the transverse membrane and the peritoneum in *Macrones*. Anteriorly to this point the peritoneum invests the ventral surface of the bilobed portion of the mesonephros, and from thence is reflected on to the posterior face of the septum separating the abdominal and branchial cavities, ultimately becoming prolonged backwards on to the dorsal wall of the œsophagus. A little in front of the outer extremity of each funnel the peritoneum grows out through the ventro-lateral muscles, and terminates in a relatively spacious cul-de-sac, between the funnel and the axilla of the pectoral fin, and immediately beneath the external skin. Each peritoneal sac contains a small diverticulum from the adjacent lateral lobe of the liver, which is connected by a slender stalk with the abdominal portion of the gland. In a somewhat similar fashion a lateral prolongation from the anterior portion of the mesonephros also bulges outwards through the ventro-lateral muscles, and occupies a recess situated just behind the mouth of the funnel and close to the superficial skin, but, unlike the hepatic outgrowths, has no peritoneal investment.

In addition to the fibrous investment which covers the osseous funnels and closes their distal apertures, the latter are also in close relation with lateral areas of the external skin. The lateral-line canal, with two of its tubular ossicles, and the lateral branch of the tenth cranial nerve, cross each area as they pass backwards from the skull.

As far as the shape and general relations of the air-bladder are concerned, TAYLOR's description (*loc. cit.*) is perfectly accurate. The organ consists of two thin-walled pyriform sacs, which occupy and completely fill the cavities of the two bony funnels (fig. 80, *a.s.*). Each sac is connected with its fellow by a narrow tubular portion which crosses the median line, ventrad to the centrum of the complex vertebra, and also to the aortic groove and dorsal aorta, and, in so doing, traverses deep emarginations in the aortic ridges.* The walls of each air-sac are everywhere in close contact with the bony or fibrous wall of its investing capsule, at all events, when the sac has not shrunken from the action of preservative fluids, or collapsed from injury to its walls. The walls of the bladder are composed of an outer fibrous sheet, the tunica externa, lined throughout by a thin delicate inner tunic with an epithelium on its inner surface. A slender ductus pneumaticus passes from the intermediate tubular portion of the bladder to the œsophagus, precisely as TAYLOR described.

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* In a specimen twelve and a half inches long, the length of each sac when measured from the middle of the tubular portion was 15 mm., and the maximum width 6 mm.

Notwithstanding the abnormal condition of the bladder, the general structure of its walls and the extent and nature of its attachments to various skeletal elements are substantially similar to those of an anterior chamber in a perfectly normal organ (fig. 81). The tunica externa of the ventral, anterior, and the greater part of the dorsal wall of each sac is extremely thin, but for a portion of its extent in the posterior wall, is somewhat thickened by the prolongation inwards between the ventral process and the transverse process of the fifth vertebra of a sheet of fibres derived from the fibrous investment of the ventral surface of the funnel which blends with the posterior wall and more or less firmly attaches the latter to the inner surface of the transverse process. In addition to this the dorsal edge of the posterior wall (*p.p.*) is firmly inserted into nearly the whole length of the posterior margin of the dorsal lamina, from the point where the latter becomes apparent as a faint ridge on the inner surface of the transverse process of the fourth vertebra in the roof of the funnel to its free inner termination in the radial nodule (*r.n.*). The median tubular section of the bladder is also attached by its anterior and dorsal walls respectively to the roots of the ventral processes and to the ventral surface of the complex centrum. Such rigid skeletal attachments are strictly comparable to the dorsal insertion of the primary transverse septum into the skeleton, and to the medio-dorsal attachment to the complex centrum, respectively, in a normal anterior chamber. The anterior pillars of the normal bladder are apparently represented in *Clarias* by the dorsal attachment of the inner or mesial portion of the anterior wall of each air-sac to the complex centrum, to the radial nodule, and to the ventral surface of the root of the crescentic process of the tripus, but unlike *Bagarius*, *Glyptosternum*, and some other abnormal Siluridæ, the remainder of the anterior wall is free from any special attachment or connection with the transverse process of the fourth vertebra.

The tripus is an unusually large but extremely thin flattened ossicle (fig. 81, *tr.*). The anterior process (*tr.a.*) is provided with a flattened inner face at its anterior extremity for the attachment of the interossicular ligament. From the junction of the anterior and crescentic processes an articular process (*tr.ar.*) is given off, which, by means of its pointed distal extremity, articulates with the lateral surface of the complex centrum at the bottom of a deep pit-like depression. Both the anterior and articular processes occupy the longitudinal groove on the lateral surface of the complex vertebra and basioccipital, and lie also in a saccus paravertebralis, the latter coinciding in position and in length with the groove itself (fig. 78, *tr.s.pv.*). The root of the crescentic process (fig. 81, *tr.c.*) enters the cavity of the corresponding funnel and curves slightly outwards into the dorsal wall of the contained air-sac as a thin tapering process of bone, and at its slender, posterior, or outer extremity becomes continuous with the apex of an equally thin, transversely elongated and somewhat triangular lamina, the broad base of which is coincident with, and parallel to, the attachment of the dorsal margin of the posterior wall of the air-sac to the confluent portion of the dorsal lamina (fig. 81). The inner portion of the triangular lamina is a trifle longer than the outer, and tapers to a point near the radial nodule, but nevertheless forms with the root of the crescentic process a characteristic concave, or rather angulated inner margin for the attachment of the radial fibres (*r.f.*) passing therefrom to the radial nodule (*r.n.*). The remaining portion of the lamina is directed outwards, like the heel-like process of *Macrones*, and also tapers to a point. The triangular lamina is the only portion of the tripus which is seen imbedded in the dorsal wall of the air-sac when the cavity of the latter is laid open from the ventral surface and the tunica interna removed. We have several times found the lamina quite distinct from the rest of the tripus, but whether normally so, or as the result of accidental fracture, we are unable to say. The slenderness of its connection with the tripus, and the extremely brittle nature of the bone itself, renders it particularly liable to separation by fracture. On the other hand, we have no doubt whatever that in many of our specimens the lamina was really continuous with the tripus, and that it represents the inwardly curved posterior section of a normal crescentic process.

The relations and attachments of the fibres forming the walls of each air-sac to the tripus are certainly more normal than we expected to find them. As previously stated, the inner or mesial portion of the anterior wall of each sac is attached by its dorsal edge not only to the radial nodule, but also to the ventral surface of the tripus, that is to say, to the root of its crescentic process, although the latter has no trace of the ventral ridge which usually marks the insertion of these fibres in the normal Siluridæ. From this point outwards the fibres of the inner stratum of the tunica externa (fig. 81, *in.st.*) in the anterior, antero-lateral, and lateral or outer walls, converge in the dorsal wall towards the tripus, and eventually are inserted into the outer margin of the crescentic process from its root to the pointed extremity of its heel-like process. The fibres of the outer stratum of the tunica externa have an almost exactly similar distribution and relation to the tripus, but pursue the usual curvilinear course in passing from their insertion into the crescentic process to the antero-lateral and lateral regions of the air-sac. The straight posterior margin of the crescentic process appears to be free from any special fibrous connection with the walls of the sac, at any rate it is certain that it does not receive the insertion of any of the converging fibres of the dorsal wall, and in this respect the tripus of *Clarias* is somewhat singular. The reason for this may possibly lie in the fact that the posterior margin of the process is almost coincident with the skeletal attachment of the dorsal edge of the posterior wall of the air-sac to the dorsal lamina.

With regard to the remaining Weberian ossicles we could detect no trace of an intercalarium, and the interossicular ligament was so short that the anterior extremity of the tripus appeared to be almost in direct contact with the outer surface of the spatulate process of the scaphium. The latter ossicle has the usual spatulate and condylar processes, but no ascending process. We could find no trace of claustra.

As far as the grosser features in the structure of the auditory organ are concerned we could detect no indication of retrogressive modification. A transverse ductus endolymphaticus and a sinus endolymphaticus are present, and the latter structure has the usual relations to the cavum sinus imparis and the atrial cavities. The closure of the external atrial aperture is effected in the usual manner by the spatulate process of the scaphium.

Clarias magur, *C. fuscus*, and *C. anguillaris*.

These species very closely resemble *C. nieuhofii* in all essential features, and, therefore, require no special description. There is, however, in each species, a fully developed, nodular intercalarium in the interossicular ligament.

Clarias macracanthus.

The anterior vertebræ and bony capsules of this species have been figured and briefly described by SÖRENSEN (37, figs. 29, 30), but no special reference is made to the air-bladder, or auditory organ. The Weberian ossicles are also figured (*loc. cit.*, figs. 31*b*, 31*b*), including a small intercalarium in the interossicular ligament.

Heterobranchus (sp ?).

We have had no opportunity of examining a species of this genus, but as the structure of the dorsal fin is almost the only point of importance in which *Heterobranchus* differs from *Clarias*, it is probable that the air-bladder and Weberian ossicles are much the same in the two genera. The only reference that we have been able to discover is by JOHANNES MÜLLER (28), whose brief description of the air-bladder of *Heterobranchus*, as being enclosed in bone, to some extent confirms our suggestion that it will be found to resemble that of *Clarias*.

GROUP :—PLOTOSINA.

Plotosus canius.

In *Plotosus* we again meet with an air-bladder of the normal type and with skeletal modifications of a very simple character.

The body of the first vertebra (fig. 82, *v.*^{1}) is free and distinct but small. The complex and fifth vertebræ (*c.c.*, *v.*^{5}) are about equal in size and firmly connected.

together, their union being due to the close sutural articulation of their respective neural arches, and to the continuous investment of their centra by superficial ossifications. The sixth vertebra (*v.*^{6}) is quite free. The spinous processes of the third and fourth vertebræ are distinct except at their roots, and incline forwards and backwards respectively. The rigid connection of the skull with the vertebral column is secured by the intimate articulation of the arch and spine of the third vertebra with the exoccipitals and supraoccipital.

The transverse process of the fourth vertebra has a broad, flat root but distally is cleft into short anterior and posterior divisions (*t.p.*^{4}*a.*, *t.p.*^{4}*p.*), of which the former is bent downwards and flattened antero-posteriorly, while the latter is somewhat expanded in a horizontal plane and angulated at its free distal extremity. The transverse process of the fifth vertebra (*t.p.*^{5}) is very similar to the posterior division of the preceding process, and at its root is partially confluent therewith. The succeeding transverse process (*t.p.*^{6}) carries the first rib (*r.*^{1}), and is quite distinct from the foregoing.

Superficial ossifications invest and considerably thicken the lateral surfaces of the complex and fifth vertebral centra, and by their produced ventral margins form the lateral walls of a median aortic groove. Anteriorly, the ossifications appear to terminate on the ventral surface of the complex centrum, near its junction with the body of the first vertebra, in a vertically disposed fan-shaped ridge, which is cleft in the centre for the transmission of the dorsal aorta (fig. 82, *sv.p.*). Dorsally, the ossifications terminate in a free edge near the roots of the contiguous transverse processes, which forms the inferior lip of a groove for the posterior cardinal vein and the anterior lobe of the mesonephros. On each of the lateral surfaces of the complex centrum, close to the root of the fan-shaped subvertebral process, there is a somewhat elongated radial nodule (*r.n.*), which is but loosely connected with the centrum by fibrous tissue, and also in the same way with a slender spicule of bone (dorsal lamina) that extends outwards beneath the posterior cardinal vein and finally blends with a longitudinal ridge on the ventral surface of the root of the transverse process of the fourth vertebra which forms the dorsal or outer margin of the cardinal groove.

The post-temporal (*pt.s.*, *pt.i.*) is normal and has the usual relations to the distal extremity of the transverse process of the fourth vertebra and the clavicle. The inferior limb (*pt.i.*) has but a slight forward inclination as it passes inwards to its articulation with the basioccipital. There are no post-temporal plates, nor is any portion of the inferior limb in contact with the anterior wall of the air-bladder.

In shape the air-bladder (fig. 83) is a flattened cone, with its broad end directed forwards and firmly buttressed laterally by the anterior divisions of the modified transverse processes, and in the median line, though to a less extent, by the fan-shaped subvertebral process. In proportion to the size of the body, the bladder is fairly large. Internally, it is subdivided in the usual way by a T-shaped arrangement of the primary transverse and longitudinal septa. The transverse septum (*t.s.*) is rather narrow. The position of its dorsal margin coincides with the commencement of the posterior third of the length of the bladder, but from this point the septum inclines obliquely forwards, so that the relatively small lateral compartments are prolonged for some distance beneath the anterior chamber. The longitudinal septum (*l.s.*) separating the two lateral chambers also extends forwards, gradually diminishing in height along the posterior face of the inclined transverse septum. The lateral edges of the transverse septum are recurved and directed backwards for a short distance parallel to each other and to the longitudinal septum. Between these recurved margins and the prolongation of the longitudinal septum on to the posterior face of the oblique transverse septum, the lateral compartments extend forwards beneath the anterior chamber in the form of two cul-de-sacs, which finally become obliterated when the two septa blend with the ventral wall of the bladder. The anterior chamber (*a.c.*), like the lateral compartments (*l.c.*) has comparatively thin walls, and for a limited portion of their extent its lateral walls are in close relation with the superficial skin. The anterior wall of the chamber is strengthened by a strong, tendinous transverse membrane which has the usual skeletal attachments laterally and dorsally, and in the median line is firmly inserted into the lateral and ventral margins of the subvertebral process. Both the anterior and lateral chambers have perfectly smooth inner surfaces, the latter being devoid of even the rudiments of secondary transverse septa. In the general disposition and skeletal attachments of the fibres forming the walls of the anterior chamber, *Plotosus* very closely resembles *Macrones.*

The scaphium has ascending, condylar, and spatulate processes. The intercalarium is a thin, discoidal nodule of bone in the interossicular ligament. The anterior and articular processes of the tripus are normal, but the crescentic process (figs. 82, 83, *r.c.*) has but a feebly marked oblique ventral ridge, and is somewhat hook-shaped, with an acutely-pointed posterior or inner extremity.

The cavum sinus imparis and its atrial cavities are perfectly normal, and the same may be said of the correlated portions of the membranous labyrinth.

As in *Clarias* the mesonephros gives off a characteristic lateral outgrowth on each side which occupies a recess in the lateral musculature of the trunk, between the external skin and the outer wall of the adjacent lateral compartment of the air-bladder.

Plotosus anguillaris.

This species differs in no essential respect from the preceding. The air-bladder is perhaps somewhat broader and deeper in proportion to its length, and its walls much thinner. The forward extension of the lateral chambers beneath the anterior compartment is even more marked than in *P. canius,* inasmuch as they reach the ventral margin of the interior wall of the bladder. From an examination of several young and half-grown examples of this species, it is obvious that the air-bladder does not always increase in size with the growth of the body, or, at all events, not to an equivalent extent. In specimens of six and twelve inches in length respectively, the bladder was exactly the same size in both cases. The mesonephric diverticula are exceptionally large, and, in conjunction with the lateral lobes of the liver, entirely exclude the outer walls of the anterior chamber from contact with their respective lateral cutaneous areas.

Copidoglanis albilabris.

As regards both its air-bladder and skeleton, this species also very closely resembles *Plotosus canius.* In size, however, the bladder is somewhat smaller in proportion to the body, and has much thicker walls. There is considerable individual variation in the size of the organ in this species. In specimens of approximately equal size the air-bladder may be a third larger in some cases than in others, but as a rule any increase or diminution in size mainly depends on the variability of the lateral compartments rather than of the anterior chamber.

Cnidoglanis megastoma.

In this species the skeletal modifications differ but little from those of the two preceding genera. The fan-shaped subvertebral process at the anterior end of the complex centrum, and the expanded and antero-posteriorly flattened anterior division of the modified transverse process, are very strongly developed, and form an almost continuous bony support to the anterior wall of the air-bladder. The posterior division of the same process, and the transverse process of the fifth vertebra, are also greatly produced and expanded, and on each side furnish a stout bony investment to the dorsal wall of the anterior chamber. The superficial ossifications extend outwards from the sides of the complex centrum as broad bony laminæ, and eventually become confluent with the ventral surfaces of the modified transverse processes, thus converting the anterior part of the cardinal groove into a complete canal.

The air-bladder is exceptionally well developed, and has large anterior and lateral compartments. Its walls are thick and of a peculiarly lustrous appearance. The primary transverse septum is inclined forwards, although not to so great an extent as in *Plotosus,* and its ventral margin is coextensive with the width of the bladder. In all other features the organ agrees with that of *Plotosus.*

The crescentic process of the tripus is not hooked but broad and thin, and in the terminal part of its rather open curvature is bent downwards and applied to the lateral surface of the complex centrum, reaching almost to the ventral margin of the latter.

GROUP :—CHACINA.

Chaca lophioides.

CUVIER and VALENCIENNES (8) describe the air-bladder of this species as very large, broader than long, and composed of two lobes, situated one on each side of the vertebral column. Its large size may, perhaps, justify the inference that the air-bladder is of the normal type.

SUB-FAMILY :—**SILURIDÆ HETEROPTERÆ.**

GROUP :—SILURINA.

Saccobranchus fossilis.

There is a short, but in some respects very inaccurate, description of the air-bladder of this species by CUVIER and VALENCIENNES (8, vol. 15, p. 301). TAYLOR (38) has also briefly referred to the organ as being very similar to that of *Clarias magur*. DAY'S account (9) is equally brief: "air-vessel tubular, placed transversely across the body of the anterior vertebræ, where it is entirely enclosed within a bony capsule" (p. 712).

With regard to the osseous capsules in which its diminutive air-bladder is enclosed, *Saccobranchus* presents an interesting gradation between *Clarias* and *Callomystax*, but the bladder itself is almost precisely similar to that of the former genus. The somewhat elongated funnel-like capsules are very similar on the whole, both in shape and mode of formation, to those of *Clarias nieuhofii*. In one or two features, however, *Saccobranchus* closely resembles *Callomystax*. The anterior margin of the transverse process of the fourth vertebra is strongly deflected throughout its entire length, but to a greater extent in its distal two-thirds, where it forms not only the anterior but also the ventral wall of each funnel, and meets behind the deflected and anteriorly-curved posterior margin of the transverse process of the fifth vertebra. As in *Callomystax*, the decurved anterior margin of the first-mentioned process unites internally with the superficial ossification investing the lateral surface of the complex centrum, and consequently converts what in *Clarias* is a mere slit for the passage of the tripus from the air-bladder to the scaphium into a complete foramen. The characteristic ventral processes which in *Clarias* help to complete the ventral walls of the funnels are absent in *Saccobranchus*, unless the slightly-retroverted edges of the lateral ridges bounding the aortic groove may be regarded as rudiments of them. The two funnels will therefore have complete bony walls except over a small area in the proximal portion of the ventral surface, and distally where they are closed only by the lateral cutaneous areas. The passage for the posterior cardinal vein (cardinal groove) is well marked on the right side, and, anteriorly both the vein and the slender anterior continuation of the mesonephros traverse a foramen in the anterior wall of the funnel situated ventrad to that which transmits the tripus. On the left side both the groove and foramen are very feebly developed. In the proximal portion of the right funnel there is a short dorsal lamina passing from the ventral surface of the transverse process of the fourth vertebra, ventrad to the cardinal groove, to unite with a well-marked radial nodule, but the latter is in close contact with the lateral surface of the complex centrum, and is somewhat loosely united thereto by fibrous tissue. On the left side, through the narrowness of the cardinal groove, the dorsal lamina is very short, and, with the radial nodule, is firmly attached to the side of the complex centrum.

In shape and structure, and in the nature and extent of its attachments to the walls of the osseous capsules and to the tripodes, the air-bladder of *Saccobranchus* closely resembles that of *Clarias*. An intermediate tubular portion connects the two lateral air-sacs, and is in communication with the œsophagus by a ductus pneumaticus.

The scaphium has a very short rudiment of an ascending process in addition to a condylar process. An intercalarium is present in the form of an extremely thin discoidal ossicle, imbedded in the interossicular ligament. The tripus (fig. 83, *a*) has a more normal shape than in *Clarias*, but its crescentic process is an exceptionally thin, wide, curved lamina of imperfectly ossified bone.

Silurus glanis.

We have but little to add to the description of this species which WEBER gave in his classical memoir, "De Aure et Auditu Hominis et Animalium, Pars i., De Aure Animalium aquatilium." On Plate V. of this memoir WEBER has given accurate figures of the membranous labyrinth and "ossicula auditus." The anterior vertebræ and their processes are also figured, but as WEBER failed to recognise the fusion of the second, third, and fourth vertebræ to form the "complex" vertebra the nomenclature he applied to them is inaccurate.

Except for the absence of a fan-shaped subvertebral process, *Silurus* closely resembles *Plotosus* in most of the osteological details with which we are now concerned, and also in the condition and skeletal relations of its air-bladder. The latter organ (fig. 84) is well developed, and its walls are fairly thick though somewhat thinner, perhaps, in the anterior chamber than elsewhere. In young specimens of from four to six inches in length the bladder is rather long in proportion to its width, but in older specimens it becomes somewhat broader and relatively shorter, and in the adult assumes the usual conical shape. The transverse septum (*t.s.*) is a narrow but stout vertical pillar of fibres, continuous behind with the longitudinal septum (*l.s.*) between the two lateral compartments. A transverse membrane with the usual lateral and dorsal attachments to the skeleton is closely applied to the anterior wall. A thin layer of fatty tissue is interposed between the outer walls of the anterior chamber and the lateral cutaneous areas.

The Weberian ossicles are also very similar to those of *Plotosus,* but the crescentic process of the tripus, like that of *Cnidoglanis* is strongly decurved towards its hinder or inner extremity and closely applied to the lateral surface of the complex centrum.

Silurus cochinchinensis.

DAY (9) thus refers to the air-bladder of this species: "Air vessel in the abdominal cavity not enclosed in bone." In all probability the organ is perfectly normal and resembles that of *S. glanis.*

Wallago attu.

There is no essential difference between this Siluroid and *Plotosus canius* or *Silurus glanis* in the structure of the air-bladder or in the character of the skeletal modification.*

The anterior division of each of the transverse processes of the fourth vertebra is strongly decurved in relation with the antero-lateral region of the air-bladder as in *Macrones,* but without being prolonged into a crescentic process. Near the distal end of the process there is an elongated concave facet for articulation anteriorly with the post-temporal. There are no subvertebral processes.

In proportion to its width the air-bladder is rather long and somewhat compressed, so that its depth is equal to, if not greater than, its width. The anterior chamber is relatively small, but on the other hand the lateral compartments are very large and extend backwards in the abdominal cavity as far as the transverse processes and ribs of the thirteenth or fourteenth vertebra. The primary transverse septum is a stout, vertical pillar produced into two ridges anteriorly as in *Arius,* which combine to form a single inwardly projecting ridge along the inner surface of the ventral wall of the anterior chamber, and eventually along the median portion of the anterior wall. The longitudinal septum is a tympaniform sheet of fibres somewhat thinner than the remaining walls of the lateral compartments.

The Weberian ossicles closely resemble those of *Cnidoglanis megastoma.*

Eutropiichthys vacha.

We have only been able to examine a skeleton of this species (fig. 85), but as our description of the modifications which the anterior vertebræ and their processes undergo in *Schilbichthys garua* (p. 211, fig. 89) will apply with scarcely any alteration to the former, it may perhaps be concluded that we have here a somewhat similar example of a vestigial and degenerate type of air-bladder. DAY (9), in his paper on the 'Freshwater Siluroids of India,' briefly refers to the air-bladder of *Eutropiichthys* in the following terms: "Air-vessel narrow, tubiform, placed transversely across the body of the anterior vertebra, and all but its central portion enclosed in bone, either expanded extremity being within a bony capsule" (*loc. cit.*, p. 713). This description does not give sufficient details to admit of comparison with other types, but taken in conjunction with the characteristic modifications of the anterior transverse processes it supports the conclusion suggested above.

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* The air-bladder of *Wallago* has been referred to by DAY (9) as follows: "Air-vessel of moderate size, situated in the anterior part of the abdomen; on removing its front wall it is found to be divided into two lateral chambers by a longitudinal septum, which, however, has a round orifice anteriorly so as to admit of free communication between the two sides."

Cryptopterus micronema.

With the exception of the two abnormal species, *C. micropus* and *C. hexapterus*, the skeletal modifications in the remaining species of the genus that we examined are almost identical with those of *Callichrous ceylonensis.** Perhaps the most striking feature in the different species of *Cryptopterus* is the marked elongation of the caudal at the expense of the abdominal region of the body, which is also accompanied by a corresponding reduction in the number of vertebræ carrying free ribs to three or four, viz., the fifth or sixth to the seventh or eighth, inclusive. The effect of this on the air-bladder is two-fold, and either leads to the backward extension of the organ into the lateral musculature of the tail, or to the assumption of a shortened and almost globose shape.

The large air-bladder of *C. micronema* is on the whole very similar to that of *Callichrous*, except that the anterior chamber is relatively small and faintly bilobed in front, while the lateral compartments gradually contract into a long, tapering, tubular prolongation which, after traversing the short abdomen, extends into the anterior third of the tail, and there lies on the right side of, and in contact with, the hæmal arches, internal to the lateral caudal muscles. The longitudinal septum is also prolonged backwards into this singular cæcal extension, and sub-divides its cavity into two lateral canals which, anteriorly, communicate with their respective lateral compartments. The walls of the bladder are very thin, and on each side, for a limited extent, the anterior chamber is in contact with a blister-like lateral cutaneous area, but this region of the body is not specially translucent.†

The Weberian ossicles, also, are very similar to those of *Callichrous;* the intercalarium has a horizontal process, but no trace of an ascending portion.

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* See p. 206.

† In this and in all the remaining species of *Cryptopterus*, the disposition and skeletal attachments of the fibres forming the walls of the anterior chamber are almost precisely the same as in *Macrones nemurus.*

Cryptopterus micropogon.

This species very clearly resembles *C. micronema*. Relatively to the large lateral chambers the anterior one is smaller than in the latter species. The walls of the bladder are much thicker than in most other species of the genus, this is principally due to the greater development of the inner stratum of the tunica externa. The dorso-lateral and ventro-lateral muscles of the trunk diverge so slightly, that the lateral walls of the anterior chamber are entirely excluded from contact with the external skin; the lateral lobes of the liver are also interposed between the two structures. As in *C. micronema* the lateral compartments are prolonged in the form of a tapering cæcal diverticulum into the anterior section of the tail. The intercalarium has a flattened expansion in the interossicular ligament, and also a horizontal process which, without forming a proper ascending portion, nevertheless curves slightly upwards into the fibrous wall of the neural canal at its inner or vertebral extremity.

Cryptopterus limpok.

In this species the relatively small air-bladder is broadly ovate or almost spherical in shape and about as deep as it is wide, the greatest depth being coincident with the position of the pillar-like transverse septum which occupies the centre of the bladder, and is continuous behind with the comparatively short longitudinal septum. The lateral walls of the anterior chamber are closely applied to the extremely thin external skin. Dr. GÜNTHER (15, p. 40) remarks of this species, that it "appears to have the place behind the head, where the air-bladder is seen through the transparent skin, of a dark colour during life." Unfortunately the intercalarium had been damaged, and we cannot therefore affirm that it is represented by more than an interossicular nodule.

Cryptopterus palembangensis.

The walls of the air-bladder, which in this species is otherwise very similar to that of *C. limpok*, are exceptionally thin and diaphanous, and in the lateral regions of the anterior chamber are in contact with large blister-like lateral cutaneous areas, thus rendering that part of the body more than ordinarily translucent.

Cryptopterus bicirrhis.

So far as the air-bladder is concerned, this species closely resembles the preceding. The intercalarium, however, not only consists of interossicular and horizontal portions, but the latter curves slightly upwards into the fibrous wall of the neural canal, and there forms a distinct rudiment of an ascending process.

Cryptopterus micropus.

We examined two badly preserved examples of *C. micropus* and *C. hexapterus*, but their condition was such that our results are necessarily imperfect, except in so far as the skeletal modifications were involved. Enough, however, could be made out to justify the conclusion that in both species the air-bladder was in an incipient stage of degeneration.

In *C. micropus* the body of the first vertebra is a mere flattened scale, and the complex centrum is but a trifle longer than the centrum of the fifth vertebra. Both the complex centrum and the basioccipital are provided with strong accessory articular processes on their ventral surfaces. A continuous deposit of superficial bone thickens the lateral surfaces of the centra of the complex and fifth vertebræ, which, otherwise, are suturally distinct from each other. There is a deep median aortic groove.

Each of the transverse processes of the fourth vertebra is partially cleft into slightly divergent anterior and posterior divisions. The anterior process has a strong ventral curvature, and a deflected anterior margin, but thins away to a somewhat pointed distal extremity. About the middle of its dorsal surface a strong process grows upwards, and is provided with an outwardly-directed facet for articulation with the post-temporal. The posterior division is directed horizontally outwards and a little backwards, and is also flattened in such a way that its surfaces look obliquely forwards towards the deflected margin of the anterior division, and backwards respectively. The comparatively slender transverse process of the fifth vertebra is partially confluent with the root of the preceding process, but for the greater part of its extent is directed outwards, parallel and slightly ventrad to the latter. In this way there is formed on each side of the complex centrum, a transversely disposed groove, open ventrally and distally, and bounded in front by the anterior division of the transverse process of the fourth vertebra, and behind by the posterior division in conjunction with the transverse process of the fifth vertebra. The sixth vertebra, and not the fifth as in the more normal species of *Cryptopterus*, carries the first pair of ribs.

A radial nodule suturally attached to the side of the complex centrum is present, and also a dorsal lamina in the usual position and with the usual relations to the posterior cardinal vein and the transverse process of the fourth vertebra.

The air-bladder is somewhat reniform in shape, with its long axis transversely disposed and the contour of its anterior wall interrupted by a deep emargination in the median line. The mesial portion of the organ lies across the ventral surfaces of the complex and fifth vertebral centra, but the more laterally situated parts occupy the grooves enclosed by the modified transverse processes, and are widely separated from the external skin. In a specimen five inches long the antero-posterior extent of the bladder was about 6 mm., and its transverse dimension about 10 mm. On removing the ventral wall it was apparent that the actual cavity of the bladder is even smaller than might be expected from its diminutive external appearance, inasmuch as the posterior half of the organ, which probably represents the partially aborted lateral compartments, is occupied by a close network of anastomosing fibrous bundles. But so far as we were able to determine, and notwithstanding these indications of degeneration, the general disposition of the fibres forming the walls of the anterior half of the bladder, and their relations to the axial skeleton and to the tripodes, are much the same as in the normal species of *Cryptopterus.* A ductus pneumaticus is present and communicates with the anterior section of the bladder.

The crescentic process of the tripus has a rather open curvature, its posterior extremity being directed but slightly inwards towards the complex centrum. The intercalarium consists of an oblong nodule imbedded in the interossicular ligament, and in our specimen was continued internally into what appeared to be the fractured rudiment of a horizontal process. The scaphium is normal, having spatulate, condylar, and ascending processes.

The cavum sinus imparis and the atrial cavities are normal, but we could arrive at no satisfactory conclusion as to the condition of the associated portions of the membranous labyrinth.

Cryptopterus hexapterus.

Except in certain minor details the anterior vertebræ and their processes resemble those of *C. micropus.* As in the latter species the transverse processes of the fourth and fifth vertebræ are modified to form on each side of the complex centrum a shallow transversely disposed groove for the reception of the corresponding lateral half of the air-bladder (fig. 86). The anterior division of the transverse process of the fourth vertebra ($t.p.^{4}a.$) is shorter and thicker than in *C. micropus,* and, instead of being produced distally into a slender decurved portion, carries the articular facet for the post-temporal at its abruptly truncated extremity. The posterior division ($t.p.^{4}p.$) is directed slightly backwards, and, in conjunction with the equally short and thick transverse process of the fifth vertebra, to which it is firmly applied, forms the posterior wall of the groove for the air-bladder. The first pair of ribs is carried by the sixth vertebra. We could detect no trace of a radial nodule or a dorsal lamina.

The air-bladder is similar in shape and general structure to that of *C. micropus,* but much smaller, its transverse extent being 5 mm., and its antero-posterior length 2·5 mm., although in each case the specimens of the two species were of approximately equal length. Its walls are extremely thick, and laterally are widely separated from the superficial skin. The lateral halves of the bladder are in free communication with each other, and also with the central portion of the œsophagus by means of a ductus pneumaticus.

The tripus and scaphium are also similar to those of the preceding species, and the intercalarium has a distinct horizontal process.

Callichrous ceylonensis.

This Siluroid bears a general resemblance to *Wallago* and *Silurus* in the structure of its air-bladder and skeleton, but some of the minor osteological details in which it differs from them indicate an approach to the *Macrones* type—a tendency which is, perhaps, better marked in some of the other species of the genus.

The body of the first vertebra is exceptionally well developed, being nearly as large as any of the normal centra that succeed the fifth. A pair of stout accessory articular processes are developed on its ventral surface for articulation with similarly situated processes on the contiguous margins of the complex centrum and basioccipital. The centra of the complex and fifth vertebræ are also of somewhat unusual length, that belonging to the "complex" being about a third the longer of the two, and both are much compressed laterally.

The anterior division of the transverse process of the fourth vertebra is much stouter than the posterior; towards its distal extremity the former carries a concave facet for articulation with the post-temporal, and is then strongly decurved and prolonged into a rudiment of the characteristic crescentic process of *Macrones* and its allies. The transverse process of the fifth vertebra is quite distinct from the foregoing, and about equal in size to the normal processes which succeed it; a slender rib is attached to its distal extremity. It will be noticed that it is the fifth, and not the sixth, vertebra, as in most other Siluridæ, which carries the first pair of ribs.

The superficial ossifications are but feebly developed, and can scarcely be said to appreciably thicken the lateral surfaces of the complex and fifth vertebral centra. Each ossification is interrupted by an irregular wavy suture as it extends over the junction of the two centra. There is a deep groove for the reception of the dorsal aorta. Anteriorly the ossifications thicken somewhat, and appear to terminate in the accessory articular processes of the complex centrum. A slightly elongated radial nodule is suturally attached to each side of the complex centrum, and to a prominence on its dorsal extremity the radial fibres of the tripus are attached. In connection with the thickened dorsal end of the nodule there is a thin spicule-like dorsal lamina having the usual relations to the cardinal groove and the transverse process of the fourth vertebra. There is no proper subvertebral process.

The inferior processes of the post-temporals have no trace of post-temporal plates.

The air-bladder is almost an exact counterpart of that of *Wallago*, and, in correlation with the laterally compressed shape of the body, is narrow, but unusually deep. The lateral walls of its anterior chamber are in close and extensive contact with the lateral cutaneous areas. In the extent and nature of the skeletal attachments of its air-bladder this genus closely agrees with *Macrones*.

The Weberian ossicles very closely resemble those of *Cnidoglanis*. The posterior and inwardly directed portion of the crescentic process of the tripus is not only bent downwards in contact with the lateral surface of the complex centrum, but is also prolonged slightly forwards to a pointed termination.

Callichrous bimaculatus.

The air-bladder, Weberian ossicles and skeletal modifications are precisely similar to those of *C. ceylonensis.* The intercalarium, however, consists of a hook-shaped process imbedded in the interossicular ligament and prolonged horizontally inwards as a slender spicule towards the membranous walls of the neural canal, thus forming a rudiment of the horizontal process of *Macrones*, but there is no trace of an ascending process. The body in the region of the lateral cutaneous areas is partially translucent.

Callichrous pabo.

This species is almost identical with the preceding in all points with which we are now concerned.

Callichrous hypophthalmus.

This species differs but little from the three preceding examples of the genus. The air-bladder is, however, less elongated and more cordate in shape, and, relatively to the size of the body, somewhat smaller. As in most other species of *Callichrous*, the lateral cutaneous areas are very thin and externally present the appearance of superficial blisters; internally, they are closely applied to the lateral walls of the anterior chamber of the bladder. The extreme thinness and transparency of these areas, and their close relation to the thin-walled anterior chamber, combined with the laterally compressed shape of the fish, have the effect of rendering this region of the body translucent when the animal is held up to the light.

The intercalarium consists of a flattened nodule in the interossicular ligament, which is prolonged horizontally inwards as a slender spicule, and eventually terminates in the fibrous wall of the neural canal, dorsad to the anterior extremity of the complex centrum, and immediately behind the condylar process of the scaphium, but there is no trace of an ascending process.

Shilbe mystus.

With the exception of one or two minor features this African Siluroid is in close agreement with *Callichrous ceylonensis*, both as regards the condition of its air-bladder and the general character of the associated skeletal modifications.

The air-bladder is less compressed than in the latter species, and, consequently, is relatively wider and not so deep. The primary transverse septum is thick but of somewhat greater transverse extent. Instead of being thin and tympaniform, the longitudinal septum is unusually stout, being strengthened by the aggregation of its component fibres into vertically arranged column-like bundles. The lateral and antero-lateral walls of the anterior chamber are somewhat thinner than the rest of the bladder and in close contact with the external skin, but this region of the body is but feebly translucent.

The Weberian ossicles also resemble those of *Callichrous,* except that the intercalarium is a slender horizontally disposed spicule, one extremity of which is bifid and imbedded in the interossicular ligament, while the other ends in the fibrous wall of the neural canal at a point a little dorsad to the anterior margin of the complex centrum.

Eutropius niloticus.

This species differs but little from the preceding. Relatively to the size of the body, the air-bladder is perhaps somewhat smaller and has thicker walls, which are not perceptibly thinner in the lateral or antero-lateral regions than elsewhere, neither is the body in any degree translucent in the region of the lateral cutaneous areas. In shape the organ is obtusely conical and somewhat flattened, with the broad end directed forwards. The intercalarium has a slender horizontal process.

Ailia bengalensis.

In this interesting Indian Siluroid the air-bladder and the co-related parts of the skeleton exhibit very singular, and in some respects, unique modifications; but the only reference to them with which we are acquainted is by DAY (9), who very briefly described the air-bladder as being very similar to that of his new genus and species *Ailiichthys punctata,* in which the organ is said to be "tubular, placed across the bodies of the anterior vertebræ, and more or less enclosed in bone" (*loc. cit.*, p. 713).

The complex and fifth vertebræ are firmly united together by the anchylosis of their neural arches and spines, as well as through the continuity of the superficial ossifications which invest the lateral surfaces of their respective centra. The sixth vertebra (figs. 87, 88, *v.*^{6}) would be quite free but for the partial coalescence of the roots of its transverse processes with those belonging to the fifth vertebra, and carries the first pair of ribs. A deep aortic groove traverses the ventral surfaces of the complex and fifth vertebral centra. The spinous processes of third, fourth, and fifth vertebræ are confluent, and form a thin, vertical and somewhat elongated lamina of bone (fig. 88, *n.s.*^{3}, *n.s.*^{4}, *n.s.*^{5}); anteriorly, the lamina has the usual articulation with the exoccipitals and supraoccipital.

The transverse processes of the fourth and fifth vertebræ (figs. 87, 88, *t.p.*^{4}, *t.p.*^{5}) are greatly expanded and confluent, forming on each side of the vertebral column a broad wing-like outgrowth. The anterior margin of each outgrowth is bent downwards in close contact with the hinder face of the skull, and the posterior margin is similarly deflected, but to a less extent (fig. 88). A very similar lateral outgrowth (figs. 87, 88, *v.p.*) is also given off on each side from the ridge bounding the aortic groove, which is nearly equal in extent and parallel to the more dorsally situated lamina formed by the expanded and confluent transverse processes. The anterior margin of each ventral outgrowth curves upwards and meets the deflected anterior edge of the transverse process of the fourth vertebra, in such a way as to form an anteriorly projecting convex surface, which is closely applied to the posterior face of the exoccipital and the adjacent portion of the epiotic. These dorsal and ventral outgrowths enclose between them, on each side, a relatively spacious recess continuous with each other posteriorly beneath the centrum of the fifth vertebra, open laterally in the dry skeleton, but closed in the fresh specimen by the lateral cutaneous area of its side, and terminating in front in a shallow bony cul-de-sac. At the anterior extremity of each cul-de-sac, and on the inner side, near the anterior end of the complex centrum, there is a small oval foramen through which the anterior process of the tripus passes to its connection with the scaphium by means of the interossicular ligament. On each side of the commencement of the aortic groove the ventral outgrowth is perforated by an oval foramen (fig. 87, *sp.n.*^{2}, *sp.n.*^{3}) for the transmission of the rami ventrales of the second and third spinal nerves, which primarily leave the neural canal between the exoccipital and the arch of the complex vertebra, and, after traversing the bony cul-de-sac, dorsad to the anterior cornu of the air-bladder, pass to their peripheral distribution through the oval foramen in question.

The post-temporal (figs. 87, 88, *pt.s.*, *pt.a.*) has no obviously distinct inferior limb for the usual articulation with the basioccipital, but it is nevertheless possible that the strip of bone disposed transversely between the foramina for the exit of the vagus (fig. 87, X) and the second and third spinal nerves may represent that element, which, presumably, has fused internally with the basioccipital, and posteriorly and externally with the conjoined anterior margins of the ventral outgrowth and the transverse process of the fourth vertebra. The ascending process (figs. 87, 88, *pt.a.*) is greatly expanded and articulates with the supraoccipital, epiotic, and pterotic bones. The stem of the post-temporal (*pt.s.*) curves obliquely backwards and downwards, and is firmly applied to the distal edge of the decurved anterior margin of the transverse process of the fourth vertebra, and to the contiguous distal margin of the ventral outgrowth (fig. 88). The distal margin of the confluent transverse processes above, and the corresponding margin of the ventral outgrowth below, in conjunction with the post-temporal stem in front, form a bony rim which is only incomplete behind, and to this rim the peripheral margins of the lateral cutaneous area of each side are attached. The socket for the clavicle is a deep groove between the post-temporal stem externally and the distal edge of the ventral outgrowth internally.

The air-bladder (figs. 87, 88, *a.b.*, *a.b.'*) is a tubular structure of fairly uniform size throughout, and consists of a transverse portion (fig. 87, *a.b.*) lying across the ventral surface of the body of the sixth vertebra, and also of two lateral cornua (fig. 88, *a.b.*') which extend forwards into the recesses between the modified transverse processes and the ventral outgrowths. Anteriorly, each cornu terminates cæcally in the shallow cul-de-sac, in which each recess ends in front, the entire bladder thus describing a horse-shoe-shaped curve with the concavity directed forwards.* The walls of the bladder are extremely thick, except towards the anterior extremities of the lateral cornua, where they become comparatively thin. The transversely disposed portion, and the immediately adjacent sections of the lateral cornua, are more or less completely filled by a delicate network of fibrous tissue, which, however, completely disappears towards the thin-walled cæcal extremities. We could detect no trace of any free or open communication between the anterior cæca through the intermediate portion, or of a ductus pneumaticus.

The skeletal attachments of the air-bladder can be more or less closely identified with those of the normal organ when allowance is made for its peculiar shape and curvature. The partially solid, intermediate section of the bladder is firmly attached to the posterior margins of the ventral outgrowths, while the inner wall of each lateral cornu is firmly connected with a thin and somewhat oblique longitudinal ridge of bone which traverses each of the lateral surfaces of the complex and fifth vertebral centra, and terminates anteriorly in a free projecting spicule, situated on the dorsal side of the thin-walled extremity of each cornu. The free spicule in all probability represents the dorsal lamina, and is almost normal in its position and relations; the longitudinal ridge itself may perhaps be regarded as an abnormal development of the oblique lateral ridge of the complex centrum, in which case its extension backwards along the lateral surfaces of the complex and fifth vertebral centra must be due to the curious infolding of the proper anterior wall of the bladder in the formation of its characteristic horse-shoe-like curvature, which has caused the ridge to lie behind, and to become confluent with, the posterior, instead of the anterior, extremity of the dorsal lamina. The hollow thin-walled extremity of each lateral cornu has much the same structure as the lateral half of an ordinary anterior chamber, and into its dorsal wall the crescentic process of the tripus is inserted. It is not possible, however, to identify any special tracts of fibres converging towards the crescentic process from the anterior and lateral walls of the cæcum, but that portion of the dorsal wall which extends from the inner edge of the process to an insertion into the free spicular extremity of the longitudinal ridge, may perhaps be considered to represent the radial fibres of other Siluridæ.

The relations of the ventral outgrowths to the air-bladder suggest that they should be regarded as due to an excessive development of such structures as are represented in a feebler degree by the characteristic ventral processes of *Bagarius*, *Glyptosternum*, and *Clarias*, or more closely perhaps by the bony laminæ which, in such extremely abnormal forms as *Loricaria Callichthys* and *Hypophthalmus* constitute the ventral walls of the bony capsules for the air-bladder. There is no trace of any superficial fibrous investment to the bladder, or of a transverse membrane, in fact, the place of these structures is really taken by the ventral outgrowths which here, as in other instances, may, with some probability, be regarded as due to the ossification of the former.

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* The width of the air-bladder was 2·5 mm., and the length measured along its curvature, 10 mm., the specimen itself being 4½ inches long.

The tripus is very similar to that of *Glyptosternum*, the crescentic process having so slight an inward curvature as to be almost straight. The intercalarium is a very small nodule of bone imbedded in the interossicular ligament. Except that it has no ascending process, the scaphium is normal.

The cavum sinus imparis and the atrial cavities differ in no essential respect from those of the more normal Siluridæ, but, unfortunately the auditory organ in the only example of this species that we were able to examine was too badly preserved to admit of any reliable results as to its structure being obtained.

Schilbichthys garua.

In its skeletal modifications this species bears some resemblance to *Cryptopterus micropus*, and also, but in a lesser degree, to *Bagarius*, *Glyptosternum*, and other similarly modified Siluroids. As we have already pointed out, the agreement between *Schilbichthys* and *Eutropiichthys* is very striking. The air-bladder is said by DAY (9) to be "small, somewhat heart-shaped, and closely attached to the bodies of the anterior vertebræ" (*loc. cit.*, p. 709).

The first, the complex, and the fifth and sixth vertebræ are rigidly connected with one another and to the skull. The body of the first vertebra is very small, and inferiorly appears to be completely enclosed within the contiguous concavities of the basioccipital and complex centrum. The length of the complex centrum (fig. 89, *c.c.*) is nearly twice that of the fifth centrum ($v.^5$), and the latter, in turn, bears about the same proportion to the normal vertebral centra which succeed it. The neural arches of the complex and two following vertebræ are confluent, or, at the most, are only partially separated by faint irregular sutures. The spine of the third vertebra is represented by a thin ridge of bone which thickens anteriorly, and slopes upwards and forwards to its articulation with the supraoccipital and exoccipital; posteriorly, the ridge is continuous with the base of the long and stout spine of the fourth vertebra, which inclines obliquely backwards, overlapping and almost suppressing the spinous process of the fifth and sixth vertebræ. The seventh vertebra ($v.^7$) is quite free.

The transverse process of the fourth vertebra ($t.p.^4$) has a broad root, slightly concave on the ventral surface, and a distal half, which is greatly expanded, and has its anterior and posterior margins curved directly downwards in such a way that they form the sides of a short but relatively deep, transversely disposed, bony semi-cylinder, the cavity of which is open distally as well as ventrally in the dry skeleton. In the fresh specimen, on the contrary, a ventral wall to each semi-cylinder is furnished by a tough fibrous membrane which stretches between, and is attached to, the decurved margins of the transverse process, and is also continued over the ventral surface of the air-bladder, while the distal apertures of the semi-cylinders are closed by the external skin. The transverse process of the fifth vertebra (*t.p.*^{5}) is a short flattened process of bone, free proximally but suturally united at its distal extremity to a small projection from the deflected posterior margin of the preceding process. The transverse processes of the sixth vertebra carry the first pair of ribs.

Superficial ossifications (*s.os.*) considerably thicken the sides, and especially the ventro-lateral margins of the complex and fifth vertebral centra, and even overlap the body of the sixth vertebra behind, as well as obscure the centrum of the first vertebra and blend with the basioccipital in front. The ventral edges of the ossifications are not only thickened but flattened out laterally so as to give rise to two longitudinal ridges the free margins of which are directed outwards. These ridges are very similar to the ventral ridges of *Bagarius*, but, while they enclose between them a shallow aortic groove (*a.g.*), do not give rise to even a trace of the ventral processes so characteristic of the last-mentioned Siluroid. There are no obvious grooves for the posterior cardinal veins, nor could we discover any trace of radial nodules or dorsal laminæ.

The post-temporal has a very slender inferior limb (*pt.i.*) which is directed obliquely forwards to its articulation with the basi-occipital, and for the distal half of its length is closely applied to the anterior wall of the semi-cylindrical transverse process. The ascending process (*pt.*, *a.*), is somewhat flattened, and has the usual articulation with the epiotic, pterotic, and supra-occipital bones of the skull. The stem of the post-temporal (*pt.*, *s.*), is deeply cleft into a long outer and much shorter inner process, which enclose between them a socket for the head of the clavicle. The inner of the two processes is firmly applied to the anterior margin of the distal aperture of the bony semi-cylinder of the same side.

In the skull the recesses for the sacculi are exceptionally small, but the cavum sinus imparis and the atrial cavities appeared to be perfectly normal.

The air-bladder (*a.b.*) is broadly ovate in shape and greatly flattened.* Along its median antero-posterior axis the bladder is perfectly solid, owing apparently to the fusion of its dorsal and ventral walls anteriorly, and to the exceptional thickness of the longitudinal septum posteriorly, and is also moulded and closely adherent to the lateral and ventral surfaces of the complex and fifth vertebral centra, more especially to the flattened-out ventral margins of the superficial ossifications. Laterally to this longitudinal partition each half of the bladder is hollow and rests by its dorsal surface on the roots of the transverse processes of the fourth and fifth vertebræ, and to some extent bulges outwards into the cavity of the corresponding bony semi-cylinder, but without completely filling the latter, or extending as far as the external skin, while its anterior and antero-lateral margins are supported by the inferior limb of the post-temporal. By these modifications the air-bladder becomes divided into two symmetrical lateral compartments by a broad, solid, and continuous longitudinal partition. We could discover no trace of a ductus pneumaticus, or of any communication between the lateral cavities. A rudiment of a transverse septum (*t.s.*) partially subdivides each cavity into a relatively large anterior moiety, and a very small posterior chamber, which intercommunicate round the free outer edge of the septum, and may be compared, the former to the lateral half of an anterior chamber, and the latter to a rudimentary lateral compartment. The transverse septum is continuous mesially with the thick longitudinal partition, and dorsally and ventrally with the corresponding walls of the bladder. The dorsal edge of the septum is firmly attached to the posterior margin of the root of the transverse process of the fourth vertebra. Notwithstanding its small size and partial encapsulation by bone, the air-bladder has extremely thick walls, composed of densely matted fibres, in which for the most part no very definite arrangement can be made out. Nevertheless, in the comparatively thin anterior portion of the dorsal wall radially arranged (*in.st.*) and curvilinear fibres may be seen, which here, as in the normal Siluridæ, converge from the anterior and antero-lateral walls of each half of the bladder to their insertion into the crescentic process of the tripus (*tr.c.*). Radial fibres may also be seen converging from the inner margin of the crescentic process, and from its ventral ridge, towards the lateral surface of the complex centrum, to which they appear to be directly attached without the intervention of a radial nodule.

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* In a specimen, eight inches long, the maximum width of the organ was 11 mm., and the length 9·5 mm.

The scaphium has no ascending process, but is otherwise normal, and its spatulate process has the usual relations to the external atrial aperture of its side. The intercalarium is a small osseous nodule in the interossicular ligament. The crescentic process of the tripus (*tr.c.*) occupies its normal position imbedded in the antero-internal portion of the dorsal wall of each half of the bladder, but has a very unusual shape. Instead of being curved, as in most Siluridæ, the process is short and broad, somewhat triangular in outline, with the apex directed backwards. The converging fibres of the dorsal wall of the bladder are inserted into a longitudinal ridge on the ventral surface of the process ; anteriorly, this ridge is continued forwards to a point near the origin of the articular process, and there receives the insertion of the usual slip of fibres derived from the mesial portion of the corresponding lateral half of the anterior wall of the bladder. The claustra are unusually well developed, and rest by their expanded bases on the dorso-lateral margins of the body of the first vertebra.

Laïs hexanema.

This Siluroid so closely resembles *Cryptopterus limpok* as regards the shape, structure, and skeletal relations of its air-bladder, that no special description of the organ need be given. Both the tripus and scaphium are normal, but the intercalarium has no horizontal process and is represented by a small bony nodule in the interossicular ligament.

Pseudeutropius.

We have not been able to examine any examples of this genus, which apparently only differs from *Schilbichthys* in the presence of a small adipose dorsal fin, but DAY (9, p. 709) briefly refers to the air-bladder of three species, viz., *P. atherinoides*, *P. murius*, and *P. goongwaree*. In the first-mentioned of these species the air-bladder is said to be of "large size, as wide as the abdominal cavity, and on removing its front wall a longitudinal septum is seen dividing it into lateral portions which, however, communicate anteriorly." The same writer remarks that in some of the larger species, such as *P. murius* (=*Eutropius* (?) *murius*), and *P. goongwaree*, "the air-vessel is larger than in *P. garua* (= *Schilbichthys garua*), and comparatively considerably smaller than in *P. atherinoides*." He also adds that "*P. garua* has the smallest air-vessel amongst the larger species which I have examined." DAY's descriptions are too brief to admit of any inferences being drawn from them, except, perhaps, that the air-bladder of *Pseudeutropius* is of the normal type and exhibits considerable variation in size in different species.

Pangasius Buchanani.

In this Siluroid we meet with several interesting features, and notably the re-appearance of an "elastic-spring" apparatus, the existence of which in the East Indian genus *Pangasius* has not hitherto been recorded. JOHANNES MÜLLER (28), in his list of those Siluridæ in which he had discovered this mechanism, not only excluded *Pangasius*, but, by implication, if not explicitly, denied its existence in this genus. TAYLOR (38) and DAY (9) have described the air-bladder of *P. Buchanani*, but they also failed to recognise the presence of the mechanism.

The body of the first vertebra is fairly well developed, being visible in the floor of the neural canal, and also on the ventral surface between the complex centrum and the basioccipital (see *P. djambal*, fig. 90, $v.^1$). The complex and two following vertebræ are rigidly connected together, partly by the superficial ossifications, and partly by the firm sutural union and partial anchylosis of their respective neural arches and spinous processes. The complex centrum is very large, exceeding in length the centra of the fifth and sixth vertebræ taken together ($c.c.$, $v.^5$, $v.^6$). The spines of the third and fourth vertebræ are united at their bases by a thin ridge of bone, but are otherwise distinct, the former inclining forwards to its connection with the supraoccipital and exoccipitals through the intervention of a considerable amount of intercalated cartilage, while the latter is directed obliquely backwards, overlapping, and to some extent suppressing, the partially confluent spines of the fifth and sixth vertebræ. The seventh vertebra is quite distinct.

The transverse process of the fourth vertebra is cleft to its root into distinct anterior and posterior divisions. The former (*tp.*^{4}*a.*), as in *Auchenipterus* and *Malapterurus*, has an oblique origin from the neural arch of the complex vertebra, and from thence curves slightly forwards, and at the same time downwards, in the form of a thin and highly elastic lamina of bone, and finally terminates by expanding into an oval plate, the long axis of which is directed from its dorsal extremity downwards, and a little outwards and forwards. The faces of the plate are somewhat oblique, but nevertheless look almost directly forwards and backwards respectively. The posterior face is nearly flat, but roughened by faint longitudinal ridges; the anterior face, on the contrary, is thickened and somewhat convex, more especially near its dorsal edge, where it becomes continuous with the elastic root. The margins of each plate are thin and extremely brittle. The protractor muscle of the plate (figs. 91, 92, *pt.m.*) has an origin similar to that of the corresponding muscle in *Auchenipterus*, and an insertion which coincides with the thickened dorsal part of the anterior face of the plate. As in other Siluroids with an "elastic-spring" apparatus, the spring and its terminal plate are widely distinct from the post-temporal, and in no way contribute to the support of the pectoral girdle. The posterior division of the transverse process (fig. 90, *tp.*^{4}*p.*) is not decurved, but forms a horizontally arranged and somewhat expanded flat plate of bone. The transverse process of the fifth vertebra (*t.p.*^{5}) is similar in shape, but more slender, and at its root slightly overlaps the preceding process. The transverse processes of the sixth vertebra (*t.p.*^{6}) are normal, and to their distal extremities the first pair of ribs (*r.*^{1}) is attached.

The superficial ossifications (fig. 90, *s.os.*) are thickest where they invest the lateral surfaces of the complex centrum, but gradually thin away posteriorly until they are reduced to comparatively inconspicuous ridges along the ventro-lateral margins of the fifth and sixth vertebral centra. Their ventral margins form two longitudinal ridges which enclose between them a well marked groove for the dorsal aorta. On each of the lateral surfaces of the complex centrum there is a short oblique ridge, and at the dorsal extremity of this a short radial nodule (*r.n.*). A dorsal lamina (*d.l.*) is prolonged from each nodule in the form of a thin obliquely disposed strip of bone, which has the normal relations to the cardinal groove (*cd.g.*), and finally blends with the ventral surface of the posterior division of the transverse process of the fourth vertebra.

As in *Auchenipterus* and *Synodontis*, and, for the same reason, the inferior limb of the post-temporal (fig. 90, *pt.i.*) is strongly developed, and has an exceptionally extensive and firm articulation with the basioccipital: the ascending process also has an equally rigid connection with the skull. The posterior face of the inferior limb is slightly hollowed out for the reception of the oval plate of the "elastic-spring" mechanism when the latter is pulled forwards by the contraction of its protractor muscle. Normally a space of about 5 mm. intervenes between the two structures, and through this interval the oval plate moves according as it is pulled forwards by the contraction of its muscle or returns to its previous position through the elastic recoil of its root on the muscle ceasing to contract.

The air-bladder (figs. 91 and 92) consists of an anterior portion, which is broad in front and oval behind, and corresponds to the whole of a normal bladder, and also of a contracted tubular part extending backwards in the substance of the kidney to within about half-an-inch of the anus. The anterior portion (fig. 91) is divided internally into a short but broad anterior chamber (*a.c.*), and two relatively large lateral compartments (*l.c.*) by the usual primary transverse (*t.s.*) and longitudinal (*l.s.*) septa. The posterior section of the bladder is a simple tubular cæcum (*p.c.*), communicating anteriorly with both the lateral chambers but terminating blindly behind. The walls of the cæcum are strengthened internally by a series of projecting annular ridges, but the longitudinal septum separating the two lateral compartments anteriorly extends into the cavity of the cæcum for only a very short distance. The cavities of the two lateral chambers (fig. 91, *l.c.*) are subdivided and greatly broken up by the formation of numerous secondary transverse septa ($t.s.^1$), which grow out from the sides of the longitudinal septum and terminate laterally in free concave margins before quite reaching the outer walls of the chambers. The secondary septa are further complicated, and the spaces they enclose additionally sacculated by the growth of numerous root-like bundles of fibres, which extend between the opposed faces of the septa, and from thence into the adjacent ventral wall of the bladder. The primary transverse septum is unusually thick, and the width of its ventral margin but a little less than that of the bladder itself (figs. 91 and 92, *t.s.*). The more contracted dorsal edge of the septum is firmly adherent to the ventral surface and sides of the posterior portion of the complex centrum, and anteriorly to this, on each side, is inserted also into the posterior margin of the dorsal lamina, while the more lateral portions of the septum have their dorsal margins attached to the ventral surfaces of the posterior divisions of the transverse processes of the fourth vertebra.

In the general structure of the walls of the anterior chamber and in the disposition and skeletal attachments of their component fibres *Pangasius* closely agrees with *Macrones* (fig. 92, *a.c.*). A noteworthy feature, however, is the thinness and transparency of its walls over a well defined oval area in each of its antero-lateral regions. The thinness of these areas is due to the extreme tenuity of the tunica externa, each area being mainly formed by the delicate tunica interna, which here, as in other Siluridæ, lines the whole of the interior of the air-bladder, including the camerated lateral compartments and the tubular cæcal appendage. To the external faces of these areas, but without being otherwise than feebly attached thereto by a delicate connective tissue, the oval plates of the "elastic-spring" mechanism are applied. The lateral walls of the anterior chamber are closely related to lateral cutaneous areas (fig. 91, *l.c.a.*), but a thin stratum of fat prevents the two structures from coming into actual contact except perhaps for a very limited extent.

A fairly strong transverse membrane invests the median portion of the anterior wall of the air-bladder, and, dorsally, is firmly attached to the ventral surface of the anterior end of the complex centrum, to its oblique lateral ridges, and to the dorsal laminæ; laterally to this point, on each side, the dorsal edge of the membrane blends with the floor of the saccus paravertebralis, while its outer edge becomes continuous with the inner and ventral margins of the oval plate of the "elastic-spring" apparatus; on the outer edge of each plate, with which it is also continuous, the membrane reappears and finally blends with the ligamentous fibres connecting the post-temporal and clavicle. Dorsally and anteriorly the membrane seems to be partially continuous with the aponeurotic membrane (fig. 91, *ap.m.*), which, after investing the dorsal surface of the anterior section of the mesonephros in the usual manner, and extending over the ventral surfaces of the inferior limbs of the post-temporals and the basioccipital, ultimately becomes continuous with the dorsal extension of the pericardio-abdominal septum. Along its entire ventral margin the transverse membrane is reflected backwards on to the ventral surface of the air-bladder, where it soon ceases to be traceable.

The relations of the oval plates of the "elastic-spring" mechanism to the transverse membrane, combined with the almost complete disappearance of the tunica externa where the plates are applied to the wall of the anterior chamber, suggests that SÖRENSEN's conclusion as to the mode of formation of the plates in *Synodontis* and *Doras* is equally applicable to *Pangasius*, and that these structures in the last mentioned Siluroid result from the ossification of both the tunica externa and the transverse membrane.

There are certain discrepancies between the brief descriptions of the air-bladder of this species given by TAYLOR and DAY, and that given by us, to which reference must be made. TAYLOR's account (38) of the bladder of "*Pimelodus pangasius*," HAM. BUCH. (= *Pangasius Buchanani*, CUV. and VAL.), is to the effect that the organ is composed of four or more portions extending in a line from opposite the pectoral fins to near the end of the tail. The first is said to be generally oval, the second pyramidal, and the two last, which run between the caudal portions of the lateral muscles, approach to a cylindrical shape. The numerous septa on its internal surface are described as descending from above downwards in the first portion, in the second they are transversely arranged, but in the posterior ones form a number of irregular cells. DAY's account (*l.c.*, p. 700) is in the following terms:—"Air-vessel large, extensive, and divided into three portions. The anterior is somewhat heart-shaped, considerably the largest, and extends from the commencement of the vertebral column to nearly opposite the posterior extremity of the pectoral fin. Its remaining portions are narrow, compressed, and continued to opposite the middle of the anal fin, amongst the muscles covering the hæmal spines It then becomes narrow and reduplicated on itself for a short distance. On removing the front wall of its first or largest portion, its interior is seen to consist of two pear-shaped cavities, the bases of which are inferior and lateral, whilst they coalesce anteriorly; the whole of the posterior half of this portion is cellular; and so is the small intermediate space between the two uncelled pyriform portions. The two posterior divisions of the air-vessel have valvular shaped folds, partially subdividing its interior." As regards the subdivision of the bladder, the two accounts are neither reconcilable with each other, nor with the description given above by us, and assuming that the specimens examined by DAY and TAYLOR were really examples of *P. Buchanani*, we can suggest no explanation of the discrepancy. Our own specimen was one from Dr. DAY's collection of East Indian Siluroids, and had been named by him *P. Buchanani*, and we may also add that its characters agreed in almost every detail with the description of this species in the British Museum Catalogue of Fishes (vol. 5, p. 62). It will be noticed, however, that both TAYLOR and DAY agree as to the extension of the air-bladder into the caudal muscles, which was certainly not the case in the specimen examined by us.

The scaphium is normal. The intercalarium is a relatively small nodule in the interossicular ligament without horizontal or ascending processes. The crescentic process of the tripus is somewhat unusually broad and flattened. From its root backwards the process is directed at first slightly outwards, and then curves inwards and downwards in contact with the lateral surface of the complex centrum, and finally in the form of a pointed process, extends slightly forwards along the ventro-lateral margin of the centrum towards the radial nodule (fig. 92, *tr.c.*). A ventral ridge traverses the root of the crescentic process, as in *Macrones*, and, anteriorly, receives the insertion of a slip of fibres derived from the mesial portion of the anterior wall of the bladder (fig. 92), and posteriorly the attachment of the fibres converging from the antero-lateral and lateral walls into the dorsal wall of the anterior chamber. Strong radial fibres (*r.f.*) pass from the inner margin of the ridge, and from the concavity of the crescent, to the radial nodule. The crescentic process is in close relation with the ventral surface of the flexible root of the "elastic-spring" apparatus, and it seems to us that the ventral curvature of the latter must restrict the lateral movements of the tripus within very narrow limits, except when the protractor muscle pulls each oval plate forwards, and consequently widens the curvature of its elastic root. Hence, as in *Auchenipterus*, the mobility of the tripus may be to some extent controlled or regulated by the action of the "elastic-spring" apparatus. The claustra are exceptionally large and somewhat triangular ossicles, with their apices extending upwards into the intercalated cartilage, which largely persists between the spinous process of the third vertebra and the exoccipitals and supraoccipital, and their broad bases resting on the lateral margins of the thick mass of fibrous tissue which forms the posterior wall of the two atrial cavities.

In the structure and relations of the auditory organ, and of the cavum sinus imparis and atrial cavities, *Pangasius* closely resembles *Macrones nemurus* and other normal Siluridæ.

Pangasius djambal.

In all osteological details (fig. 90) this species is practically identical with *P. Buchanani*, but in the structure of the air-bladder the former presents one or two minor points of divergence from the latter.

The air-bladder of *P. djambal* (fig. 93) consists of an anterior portion subdivided in the usual way into an anterior (*a.c.*) and two lateral (*l.c.*) compartments, and also of a posterior cæcal appendage (*p.c.*). The latter is not tubular, as in *P. buchanani*, but has the shape of an elongated, flattened, oval structure, and extends nearly to the hinder extremity of the abdominal cavity, being separated from the rest of the bladder anteriorly by a deep constriction; from its posterior end a small cæcal protuberance ($p.c.^1$) is given off, which is less than half an inch in length, and gradually tapers to a point near the anus. The cavity of the cæcal appendage (*p.c.*) is largely filled up by a network of fibrous bundles, some of which are vertically and others horizontally arranged, the whole forming a coarse trabecular structure and subdividing the cavity into a series of intercommunicating spaces. The network seems to owe its formation to the disintegration of a median longitudinal septum and several secondary transverse septa. In a somewhat similar fashion the longitudinal septum (*l.s.*), and the secondary transverse septa ($t.s.^1$) of the two lateral compartments are broken up into a series of not very regularly arranged vertical columns, which dorsally and ventrally pay out into root-like bundles and extend into the adjacent dorsal and ventral walls. As far as the tunica externa is concerned these septa are certainly not continuous structures, and hence the spaces they enclose appear to be in direct and free communication with one another. It is possible, however, that the tunica interna may preserve the continuity of the septal elements and the distinctness of the lateral chambers, except of course where the latter are continuous through the anterior chamber, but we are not absolutely certain on this point. Except where the oval plates of the "elastic-spring" mechanism ($t.p.^4a.$) are applied to the lateral regions of the anterior wall of the bladder, the latter organ has much thicker walls than is the case with any of the other species of *Pangasius* that we examined. Fig. 94 represents the tripus of this specimen.

Pangasius macronema.

This species exhibits a general resemblance to the two preceding species in the structure of the air-bladder and the character of its "elastic-spring" apparatus.

The anterior division of each of the modified transverse processes has a slender stalk-like root, which, after a very slight ventral curvature, expands into a large but very thin oval plate. Each plate has its long axis transversely disposed, and its posterior face, which looks directly backwards, is closely applied to the corresponding lateral half of the anterior wall of the air-bladder.

The air-bladder itself has thin walls, and consists of an anterior and somewhat rounded portion, which includes the anterior and two lateral compartments, and in addition also, a posterior much flattened, leaf-like cæcum connected with the foregoing by a short tubular stalk. The cavities of both the lateral compartments and the posterior cæcal appendage are largely occupied by a trabecular network of branching columns of fibres, but the outer portions of the former are comparatively free from such bundles, and communicate in front with the anterior chamber. As in *P. djambal* this network seems to owe its formation to the partial resolution of a series of secondary transverse septa into branching bundles of fibres. The wall of the anterior chamber is not specially thin where the oval plates of the "elastic-spring" mechanism are applied to it, and it may therefore be inferred that, as in *Malapterurus*, according to SÖRENSEN, the plates result from the ossification of the transverse membrane alone, the tunica externa having no share whatever in their formation.

Pangasius micronema.

In a specimen from Dr. BLEEKER's collection labelled *P. micronema*, and agreeing in every particular with the description of this species in the British Museum Catalogue of Fishes (vol. 5, p. 63), we noticed one or two features in which it presented a striking contrast to all other species of the same genus that had come under our notice.

Each of the transverse processes of the fourth vertebra (fig. 96) has a broad flat root, which is prolonged distally into distinct anterior ($t.p.^4a.$) and posterior ($t.p.^4p.$) divisions, separated from each other by a broad but comparatively shallow cleft. The anterior division ($t.p.^4a.$) is thick and inflexible, tapering somewhat towards its decurved distal extremity, but is without a trace of the oval plate so characteristic of other species of *Pangasius*; on the contrary, and as in most other Siluridæ not provided with an "elastic-spring" mechanism, the distal portion of the process is applied to, and firmly supports the outer extremity of the inferior limb of the post-temporal (*pt.i.*), and also the inner of the two processes into which the cleft stem of that bone (*pt.s.*) divides in forming the socket for the clavicle ($c.^1$). Hence, in this species, the transverse process of the fourth vertebra is not modified to form an "elastic-spring" apparatus, but both in shape and in the support which it affords to the post-temporal and pectoral girdle, closely conforms to its normal condition in the great majority of the Siluridæ; and in harmony with this modification, is the fact that the inferior limb of the post-temporal is relatively slender, or at all events is nothing like so massive as in other species of *Pangasius*.

The air-bladder is broadly ovate in shape but rendered slightly bilobed in front through the existence of a deep median notch in its anterior wall. Relatively to the lateral compartments the anterior chamber is very small, and there is no posterior cæcal appendage. The walls of the bladder are extremely thin. The primary transverse septum is so obliquely placed that, while its lateral portions are vertical and directly-continuous with the ventral wall of the bladder, the median part is inclined downwards and forwards, and does not finally blend with the ventral wall until it almost reaches the inferior margin of the anterior wall. Through the obliquity of the septum, the lateral compartments and the longitudinal septum separating them are prolonged beneath the median portion of the anterior chamber nearly as far forwards as the anterior wall of the latter. The structure and skeletal attachments of the anterior chamber are otherwise perfectly normal. The inner half of each lateral compartment is subdivided by numerous secondary transverse septa, and these, with the root-like bundles which they give off dorsally and ventrally, largely obliterate the cavity of this part of the bladder. The outer portions of the compartments, on the contrary, are comparatively open and freely communicate in front with the cavity of the anterior chamber.

The Weberian ossicles resemble those of other species of *Pangasius*, except that the inner extremity of the crescentic process of the tripus is not prolonged forwards towards the radial nodule in the form of a pointed projection.

Pangasius juaro.

This species substantially agrees with *P. macronema* in almost every respect. The flexible root of each "elastic-spring" apparatus (fig. 95, *t.p.^{4}a.*) is, however, even more slender, and the oval plate in which it terminates exceptionally large and extremely thin. In our solitary specimen there was no posterior cæcum in connection with the normally subdivided portion of the bladder, but, as the Fish had been eviscerated before it came into our possession, it is possible that the cæcum had been removed with the stomach and intestines. From the appearance of the posterior extremity of the bladder we incline to the opinion that a posterior cæcal appendage does normally exist in this as in other species of *Pangasius* in which the "elastic-spring" mechanism is present. In the relative proportions of the anterior and lateral compartments, and in the growth of a trabecular network of branching bundles of fibres in the latter, *P. juaro* closely resembles *P. macronema.*

Silondia gangetica.

Our solitary example of this species was a very young specimen about seven inches in length, and was one of the Indian Siluroids given to us by Dr. DAY. The air-bladder has been briefly described by TAYLOR (38) as being very small in proportion to the bulk of the Fish. It is said to lie close to the anterior vertebræ, to be oval in shape, and divided internally into two cavities, each of which, in a Fish weighing eight pounds, was not larger than a hazel nut. There is also a brief reference to the organ by DAY (9) in the following terms:—"Air-vessel small and placed transversely across the body of the anterior vertebra, where there is a groove to receive its posterior surface; anteriorly, it has a thick strong fibrous covering. There is a low osseous process from the vertebra giving it protection laterally. The air-vessel itself consists of two small oval portions, having a median connecting tube, and this lateral part is surrounded by osseous or strong fibrous walls" (*loc. cit.*, p. 712). As the species may attain a length of four feet, it is obvious that our specimen was a very immature one, but this fact alone can hardly account for the marked discrepancy between the conflicting statements of these writers, and the results of our own dissections as stated below.

The body of the first vertebra is a thin discoidal bone with but slightly concave anterior and posterior surfaces, and quite distinct from the complex centrum and basioccipital. The complex and fifth vertebræ alone are rigidly connected together by the superficial ossifications and the partial anchylosis of their neural arches. The sixth vertebra is quite free. The spines of the third and fourth vertebræ form a thin vertical plate of bone with thickened and produced anterior and posterior margins. The anterior margin is inclined forwards and bifid; occupying the cleft, and connecting the spine with the supraoccipital and exoccipital bones of the skull, is a considerable amount of intercalated cartilage. The posterior margin is inclined obliquely backwards and deeply cleft for the support of certain of the anterior interspinous bones of the dorsal fin.

The flat roof of the transverse process of the fourth vertebra splits distally into an anterior and a posterior division, the former (fig. 97, *t.p.*^{4}*a.*) curving downwards and supporting the anterior wall of the bladder, and in front articulating by a well-marked facet with the post-temporal so as to complete the socket for the clavicle. The slender transverse processes of the fifth and sixth vertebræ (*t.p.*^{5}, *t.p.*^{6}) are widely distinct from the foregoing; proximally, they are slightly confluent but their distal extremities are quite free. The sixth vertebra carries the first pair of ribs (r^1).

The ventro-lateral margins of the complex and fifth centra are greatly thickened by superficial ossified deposit, which is prolonged ventrally on each side to form the lateral walls of a median aortic groove. The dorsal lamina (fig. 98, *d.l.*) is represented by a slender spicule of bone, which on each side becomes detached from the ventral surface of the transverse process of the fourth vertebra, close to the complex centrum, and, after a slightly oblique course forwards and downwards, ventrad to the posterior cardinal vein of its side, terminates in a free anterior or ventral extremity which receives the insertion of the radial fibres of the tripus.

The air-bladder (fig. 97) has a very unusual structure. In shape it is somewhat reniform, with its long axis transversely disposed and its anterior wall very slightly concave, while its posterior contour is strongly convex.* The lateral portions of the anterior wall are supported by the deflected anterior divisions (*t.p.*^{4}*a.*) of the modified transverse processes. There is no divergence of the dorso-lateral and ventro-lateral muscles, and consequently the lateral walls of the bladder are widely separated from the external skin. On removing the ventral wall a thick and almost circular pillar of fibres is seen to extend vertically between the dorsal and ventral walls, thereby reducing the actual cavity of the bladder to the condition of a comparatively narrow circular canal surrounding the central pillar (*t.s.*). The antero-lateral portions of the canal are very slightly dilated, and into the dorsal wall of these regions the crescentic process of the tripus is on each side inserted in the normal fashion, but otherwise the calibre of the canal is fairly uniform throughout. Dorsally, the central pillar is closely moulded to the ventral and lateral surfaces of the centra of the complex and fifth vertebræ, and firmly adherent thereto, while the lateral portions of the bladder are applied to the ventral surfaces of the transverse processes of the fourth and fifth vertebræ. We can only regard the formation of the vertical pillar as due to an excessive thickening of the primary transverse septum, and possibly also of the anterior portion of an incomplete longitudinal septum, with the necessary result that the central or mesial portions of the bladder cavities have to a great extent become obliterated. As in the more normal types, the cavity of the air-bladder has a thin but continuous lining of tunica interna. Notwithstanding the degenerate condition of the bladder, the disposition and arrangement of the fibres forming the comparatively thin antero-lateral walls of the circular canal and their convergence in the dorsal wall to their ultimate insertion into the crescentic processes of the tripodes (fig. 98), are substantially the same as in a normal anterior chamber. Radial fibres (*r.f.*) may also be seen passing from the concavity of each crescentic process (*t.r.c.*), and, in the absence of a radial nodule, becoming attached to the free extremity of the spicular dorsal lamina (*d.l.*). We could detect no trace of a ductus pneumaticus.

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* The dimensions of the bladder in our specimen were, width 10 mm., length 9 mm.

The tripus has the usual three processes, but the crescentic process (fig. 98, *t.r.c.*) is very slender and has only a slight inward curvature. The scaphium is quite normal, having completely formed spatulate, condylar, and ascending processes. The intercalarium is a very feebly developed nodule in the interossicular ligament. Claustra are present with their dorsal extremities projecting into the intercalated cartilage between the spine of the third vertebra and the supraoccipital and exoccipital.

We were unable to make any satisfactory examination of that part of the internal ear which is specially related to the Weberian mechanism, but the cavum sinus imparis and its atrial diverticula, as well as the relations of the latter to the scaphia, were perfectly normal.

IV.—MORPHOLOGICAL SUMMARY.

In summarising the more noteworthy of the results of our investigations into the morphology of the air-bladder and Weberian ossicles, and the correlated modifications which the anterior vertebræ and their processes undergo, we may indicate, in the first instance, such features as appear to be common to nearly all Siluroids, and secondly, those that are characteristic of particular genera or species.

Although only demonstrated in one particular instance (the young of *Amiurus catus*) by RAMSAY WRIGHT, our researches lead us to believe that the great majority of Siluroids agree with *Amiurus* in having the centrum of the second vertebra, and the centra, neural arches, and spinous processes of the third and fourth vertebræ indistinguishably combined to form an apparently single vertebra, for which we have ventured to suggest the name of "complex vertebra." The discovery by BAUDELOT that the "complex vertebra" of the Cyprinidæ was formed by the fusion of the second vertebral centrum with the third vertebra, was due to the distinctness of these elements in one particular species, but no evidence of a similar nature is available in any but embryonic Siluridæ. In no adult Siluroid is there the slightest trace of intervertebral spaces or sutures between the three confluent centra; in fact, the only features which in any way suggest the composite nature of the complex vertebra in that family are the perforation of its neural arch by two pairs of spinal nerves and the occasional presence of two pairs of nutrient foramina on the ventral surface of its centrum. Nevertheless the constancy of its characters in nearly all Siluridæ and the suppression of all trace of the second vertebral centrum as a distinct element, justifies the conclusion that the complex vertebra has the same value as in *Amiurus*. This fusion of vertebræ in the formation of the "complex" is almost invariably attended by the partial anchylosis of the latter to the fifth vertebra, partly as the result of the firm sutural union of their correlated elements and in part due to the investment of the lateral surfaces of their centra by a continuous deposit of superficial bone. Moreover, the conjoined vertebræ, with the addition of the centrum of the first, are so articulated to the skull that little, if any, motion is possible, either between the individual vertebræ or between the latter and the skull. The centrum of the first vertebra is nearly always much smaller than any of the normal centra.

With the possible exception of the claustra, no distinct or ossified intercalary elements are ever present.

The first vertebra very rarely has transverse processes, and even when present (*e.g.*, some species of *Arius*) they are extremely rudimentary. Unless represented by the horizontal processes of the intercalarum in some Siluridæ (*e.g.*, *Macrones*) and the tripodes, respectively, the second and third vertebræ are always devoid of transverse processes. The transverse processes of the fourth vertebra, on the contrary, are always greatly expanded, not infrequently divided into anterior and posterior divisions by a cleft, and with or without the aid of those belonging to the fifth vertebra form a more or less complete investment to the dorsal and anterior walls of the air-bladder. The sixth is, as a rule, the first rib-bearing vertebra; exceptionally, however, the first rib may be borne by the fifth, or even the seventh vertebra.

In almost all cases, except where they are modified to form an "elastic-spring apparatus," the transverse processes of the fourth vertebra, in addition to their characteristic relations to the air-bladder, form a more or less rigid support to the proximal elements of the pectoral girdle.

Over a somewhat triangular area, on each side, between the exoccipital in front and the anterior margin of the arch of the complex vertebra behind, the wall of the neural canal is formed only by fibrous membrane, in which the claustrum, and the ascending processes of the scaphium and intercalarium when present, are imbedded.

Of the four Weberian ossicles the claustrum has no physiological relations to the atrial cavities (atria sinus imparis of WEBER), but merely strengthens the wall of the neural canal behind the exoccipital. Each scaphium has a spatulate process which fits into and completely closes the corresponding external atrial aperture, and at the same time forms the outer wall of the atrial cavity of its side, and usually also a rounded condylar process for articulation with the centrum of the first vertebra. The intercalarium is generally represented by an elongated or discoidal nodule imbedded in the stout ligament ("interossicular ligament") connecting the scaphium with the tripus, and even if horizontal and ascending processes are present, the ossicle never articulates in the adult with the centrum of the second vertebra, to which, as a modified neural arch, it belongs. The tripus is always a tripartite ossicle with its posterior or crescentic process imbedded in the dorsal wall of the air-bladder; the anterior process is directed forwards parallel to the long axes of the complex and first centra, and opposite the external atrial aperture of its side is connected by the transversely-disposed interossicular ligament with the convex outer surface of the spatulate process of the scaphium. The articular process usually articulates with the lateral surface of the third vertebral centrum, to which, as a modified transverse process or rib, the tripus probably belongs; very rarely (*e.g.*, *Auchenipterus*) is the process directly continuous with the neural arch.

The Weberian ossicles, or at all events the free portion of the tripus and the intercalarium, are enclosed within a membranous saccus paravertebralis, the anterior wall of which is perforated by the interossicular ligament as the latter passes inwards from the tripus to its attachment to the scaphium. Unlike the Cyprinidæ, the complete closure of the external atrial aperture by the spatulate process of the scaphium and the minute size of the hypoglossal foramen in the Siluridæ completely cut off all communication between the cavity of the saccus and the cranial cavity.

With the exception, perhaps, of the Hypophthalmina and the Hypostomatina, the relations of the anterior spinal nerves to the vertebral elements with which they are associated is remarkably constant.

The first spinal or hypoglossal nerve perforates the exoccipital. The second and third spinal nerves emerge from the neural canal between the claustrum anteriorly and the arch of the complex vertebra behind, but are invariably separated by the ascending process of the intercalarium whenever that process is developed, as in *Macrones, Liocassis,* and *Bagroides.* The fourth and fifth spinal nerves traverse the neural arch of the complex vertebra, and the sixth the arch of the fifth vertebra. The additional spinal nerve described by SAGEMEHL in *Silurus glanis* as emerging between the claustrum and the ascending process of the scaphium, we have never met with, although our attention has been specially directed to that point.

The air-bladder varies greatly in degree of development, not only in different genera, but in different species of the same genus. Even individual variations are not infrequent, but it never exhibits that bipartite division into simple anterior and posterior sacs which is so characteristic of all other families of Ostariophyseæ. One of its most noteworthy features is a tendency to lateral development, whereby the outer walls of the anterior portion become applied, through the divergence of the dorso-lateral and ventro-lateral muscles of the body wall, directly to the external skin ("lateral cutaneous areas"). The insertion of the crescentic processes of the tripodes is always into the dorsal wall of the anterior chamber of the air-bladder in the normal Siluridæ, or into the corresponding walls of the laterally situated air-sacs in the abnormal forms, and, as a rule, takes place in such a way that the fibres forming the anterior and lateral walls of each half of an anterior chamber, or of each air-sac, converge as they pass into and form the dorsal wall, and ultimately become inserted into the convex outer margin of the tripus of that side. Specialised fibres of the dorsal wall ("radial fibres") converge like the radii of a circle from the inner concave margin of the crescentic process, and are inserted either directly into the adjacent lateral surface of the complex centrum or indirectly through the intervention of an osseous nodule ("radial nodule").

In nearly all Siluroids the lateral growth of the air-bladder, and the intimate relation of its outer walls to the lateral cutaneous areas, have led to the displacement of the lateral lobes of the liver and their enclosure within peritoneal cul-de-sacs, a condition which sometimes persists even in cases where the air-bladder has undergone partial atrophy.

In no Siluridæ are special capillary tufts or retia mirabilia (the so-called vaso-ganglia), invested by a special modification of the epithelium of the tunica interna, ever developed in connection with the air-bladder.

As a convenient means of summarising the more important generic and specific variations, the Siluroids may be somewhat arbitrarily divided into two principal groups:—(1) the *Siluridæ normales,* and (2) the *Siluridæ abnormales.* In the former group the air-bladder is always well developed and subdivided internally into three intercommunicating compartments, of which one is anterior, and two posterior and lateral in position. The anterior and dorsal walls of the anterior chamber may be more or less completely invested by the modified transverse processes of the fourth and fifth vertebræ, but the latter do not form deep concave recesses or capsules for the partial or complete enclosure of the entire air-bladder.

In the Siluridæ abnormales on the contrary, the air-bladder is always very small, or even diminutive, relatively to the size of the Fish, and more or less degenerate, sometimes partially solid, but almost invariably includes two laterally situated air-sacs with simple cavities, which together may be regarded as equivalent to the anterior chamber in a normal Siluroid. Lateral compartments, as a rule, are absent altogether, or, if present, are very rudimentary. Whatever its condition, the air-bladder is almost always partially or completely enclosed within transversely disposed bony recesses, formed either by the transverse processes of the fourth vertebra alone, or in conjunction with those of the fifth vertebra.

Although a convenient method of classifying morphological facts, it is obvious that this classification, based as it is upon so variable an organ as the air-bladder, can have no genetic value.

1. *Siluridæ Normales.*

Under this head may be included the genera: *Plotosus*, *Copidoglanis*, *Cnidoglanis*, *Silurus*, *Wallago*, *Cryptopterus* (certain species), *Callichrous*, *Schilbe*, *Eutropius*, *Pangasius*, *Bagrus*, *Macrones*, *Pseudobagrus*, *Liocassis*, *Bagroides*, *Rita*, *Amiurus*, *Platystoma*, *Piramutana*, *Pimelodus* (certain species), *Auchenoglanis*, *Arius*, *Hemipimelodus*, *Ketengus*, *Ælurichthys*, *Osteogeniosus*, *Batrachocephalus*, *Auchenipterus*, *Malapterurus*, *Oxydoras*, *Laïs*, and *Aspredo.*

In the Siluroids included in this group the number of rigidly interconnected vertebræ varies. The first, the complex, and the fifth vertebræ are invariably so connected together that no motion is possible between them; and occasionally the sixth, the seventh, and even the eighth, may be included in the series. The firmness of their union naturally varies with the age of the specimen, being greater in mature or old specimens than in young ones, but prolonged maceration generally has the effect of rendering all but the complex and fifth vertebræ more or less easily separable. The rigid connection of these vertebræ is effected by various means, of which the investment of the lateral surfaces of their centra by a continuous deposit of superficial bone, and the firm sutural union, or even partial anchylosis, of their neural arches and spines, are the most noteworthy. The rigidity of the complex and fifth vertebræ, with the occasional addition of the sixth, may be further increased by the sutural union or partial anchylosis of their respective transverse processes. The anterior vertebræ are also firmly connected to the skull, generally by the articulation of the arch and spine of the third vertebra with the exoccipitals and supraoccipital, the transverse processes of the fourth vertebra with the post-temporals, and the spinous processes of the third and fourth vertebræ with the supraoccipital spine; less frequently by the formation of interlocking accessory articular processes on the contiguous ventral margins of the basioccipital and the centra of the first and complex vertebræ. In some Siluroids the same result is secured by the downward growth and coalescence of the accessory processes, to form a stout subvertebral process. In other Siluroids the connection of the skull with the anterior vertebræ may be rendered still more intimate by the articulation of the spine of the supraoccipital with the expanded dermal plates of the first and second interspinous bones (*e.g.*, *Auchenipterus*, *Oxydoras*, &c.), or even by the extension of bony laminæ between the supraoccipital and the dorsal surfaces of the transverse processes of the fourth vertebra (*e.g.*, *Arius*, *Batrachocephalus*, *Osteogeniosus*, and *Ketengus*).

The centrum of the first vertebra varies greatly in size, but is always smaller than any of the other anterior vertebral centra. Two pit-like sockets are always found on its dorsal surface for the reception of the condylar processes of the scaphia. The complex and fifth centra are the largest, or at all events the longest, of the anterior centra, and, as a rule, their anterior and posterior concavities are unsymmetrically developed. In nearly all cases these centra are not only elongated, but laterally compressed, so as to form a prominent subvertebral keel, which gives rise to a deep groove along the medio-dorsal line of the anterior chamber of the air-bladder, and, at the same time, internally, to a well marked longitudinal ridge partially subdividing the cavity of the chamber into two laterally bulging halves. As a rule the centrum of the complex vertebra is much longer than the centrum of the fifth vertebra, although, exceptionally, it may be shorter than the latter (*e.g.*, *Platystoma*). Its concavities may be subequal (*Arius*), but more frequently the posterior is much the deeper of the two, and may even be almost tubular. One (*Macrones*) or two (*Synodontis*) pairs of nutrient foramina are present on its ventral surface, and apparently belong to the third and fourth vertebræ. A pair of accessory articular processes may be developed on the anterior margin of the ventral surface of the complex centrum, and may interlock with similar paired processes developed from the adjacent margins of the basioccipital and the centrum of the first vertebra (*e.g.*, *Macrones*). The centrum of the fifth vertebra is generally shorter than the complex centrum, but in one or two instances (*e.g.*, *Platystoma*) it may equal or exceed the latter in length. Its two concavities are rarely subequal; more frequently the anterior is much the deeper, and sometimes may be even tubular (*e.g.*, *Aspredo*, *Platystoma*). The sixth vertebral centrum is also nearly always larger than any that succeed it, although smaller than either the complex or fifth centrum. Its concavities are equal or subequal, but occasionally, as in the fifth, the anterior may be much deeper than the posterior.

The neural arch of the complex vertebra is always represented by two lateral and continuous plates of bone, confluent above with the spines of the third and fourth vertebræ and below with the centrum. The lateral vacuities, which in some Siluridæ (*e.g.*, *Platystoma* and *Auchenoglanis*) partially interrupt the continuity of the arch, may possibly indicate a separation between the otherwise confluent arches of the third and fourth vertebræ. As a rule, the arch is partially or completely anchylosed to that of the fifth vertebra, which in turn may be similarly connected with the arch of the sixth vertebra, or the rigid union of the different neural arches may be effected by a firm sutural union only. Even when not actually anchylosed it is rare for the arches of the fifth, sixth, or seventh vertebræ to be movably articulated by means of pre- or post-zygapophyses as is the case with the normal free vertebræ that follow.

The spinous processes of the third and fourth vertebræ are either confluent to form a thin vertical lamina of bone (*Macrones*), or fused only at their roots, their distal extremities being free and divergent (*Arius*). The spine of the third vertebra is almost always grooved anteriorly and inclined forwards over the body of the first vertebra to an articulation with the exoccipitals and supraoccipital; in the groove a modicum of intercalated cartilage is very generally present, more especially in young or immature specimens. The spine of the fourth vertebra is usually directed backwards and, like the succeeding spines, is generally cleft for the support of certain of the interspinous bones of the dorsal fin, but in the absence of the latter may, like its fellows, be simple and undivided (*e.g.*, *Malapterurus*). The spines which immediately succeed the foregoing may be rudimentary or obsolete (*Arius*), or well-developed and bifid; not infrequently they are either partially anchylosed or firmly articulated to one another and to their predecessors.

The transverse processes of the fourth vertebra, very frequently those of the fifth, and more rarely those belonging to the sixth vertebra (*Platystoma*), are more or less expanded and by their partial anchylosis or sutural union form on each side of the vertebral column a broad wing-like plate of bone, the anterior margin of which is strongly decurved, for the investment of the anterior and dorsal walls of the anterior chamber of the air-bladder. The transverse process of the fourth vertebra has a broad flat root, and for the rest of its extent may be simple, or, as is more usually the case, cleft more or less deeply into distinct anterior and posterior divisions, of which the former is always strongly decurved towards its distal extremity and closely applied, even if not attached, to the lateral portion of the anterior wall of the air-bladder. The anterior division is usually applied distally to the inferior limb and stem of the post-temporal, and firmly united thereto by a ligament in such a way as to afford a rigid support to the proximal portion of the pectoral girdle. The entire transverse process invariably has its origin, not from the centrum, but from the whole length of the continuous neural arch of the complex vertebra. In certain Siluroids this process becomes modified to form the singular "elastic-spring" apparatus first described by JOHANNES MÜLLER. In some of these forms (*Malapterurus, Synodontis, Pangasius*) each anterior division is almost completely separated from the posterior division, with an oblique origin from the arch of the complex vertebra, and becoming flexible and highly elastic, expands distally into an ovoid plate which is closely applied to the corresponding lateral portion of the anterior wall of the air-bladder. In others (*e.g.*, *Oxydoras* and *Auchenipterus*) the anterior division undergoes a similar modification, but the posterior division has become completely suppressed. In all such contiguous ventral margins of the basioccipital and the centra of the first and complex vertebræ. In some Siluroids the same result is secured by the downward growth and coalescence of the accessory processes, to form a stout subvertebral process. In other Siluroids the connection of the skull with the anterior vertebræ may be rendered still more intimate by the articulation of the spine of the supraoccipital with the expanded dermal plates of the first and second interspinous bones (*e.g.*, *Auchenipterus*, *Oxydoras*, &c.), or even by the extension of bony laminæ between the supraoccipital and the dorsal surfaces of the transverse processes of the fourth vertebra (*e.g.*, *Arius*, *Batrachocephalus*, *Osteogeniosus*, and *Ketengus*).

The centrum of the first vertebra varies greatly in size, but is always smaller than any of the other anterior vertebral centra. Two pit-like sockets are always found on its dorsal surface for the reception of the condylar processes of the scaphia. The complex and fifth centra are the largest, or at all events the longest, of the anterior centra, and, as a rule, their anterior and posterior concavities are unsymmetrically developed. In nearly all cases these centra are not only elongated, but laterally compressed, so as to form a prominent subvertebral keel, which gives rise to a deep groove along the medio-dorsal line of the anterior chamber of the air-bladder, and, at the same time, internally, to a well marked longitudinal ridge partially subdividing the cavity of the chamber into two laterally bulging halves. As a rule the centrum of the complex vertebra is much longer than the centrum of the fifth vertebra, although, exceptionally, it may be shorter than the latter (*e.g.*, *Platystoma*). Its concavities may be subequal (*Arius*), but more frequently the posterior is much the deeper of the two, and may even be almost tubular. One (*Macrones*) or two (*Synodontis*) pairs of nutrient foramina are present on its ventral surface, and apparently belong to the third and fourth vertebræ. A pair of accessory articular processes may be developed on the anterior margin of the ventral surface of the complex centrum, and may interlock with similar paired processes developed from the adjacent margins of the basioccipital and the centrum of the first vertebra (*e.g.*, *Macrones*). The centrum of the fifth vertebra is generally shorter than the complex centrum, but in one or two instances (*e.g.*, *Platystoma*) it may equal or exceed the latter in length. Its two concavities are rarely subequal; more frequently the anterior is much the deeper, and sometimes may be even tubular (*e.g.*, *Aspredo*, *Platystoma*). The sixth vertebral centrum is also nearly always larger than any that succeed it, although smaller than either the complex or fifth centrum. Its concavities are equal or subequal, but occasionally, as in the fifth, the anterior may be much deeper than the posterior.

The neural arch of the complex vertebra is always represented by two lateral and continuous plates of bone, confluent above with the spines of the third and fourth vertebræ and below with the centrum. The lateral vacuities, which in some Siluridæ (*e.g.*, *Platystoma* and *Auchenoglanis*) partially interrupt the continuity of the arch, may possibly indicate a separation between the otherwise confluent arches of the third and fourth vertebræ. As a rule, the arch is partially or completely anchylosed to that of the fifth vertebra, which in turn may be similarly connected with the arch of the sixth vertebra, or the rigid union of the different neural arches may be effected by a firm sutural union only. Even when not actually anchylosed it is rare for the arches of the fifth, sixth, or seventh vertebræ to be movably articulated by means of pre- or post-zygapophyses as is the case with the normal free vertebræ that follow.

The spinous processes of the third and fourth vertebræ are either confluent to form a thin vertical lamina of bone (*Macrones*), or fused only at their roots, their distal extremities being free and divergent (*Arius*). The spine of the third vertebra is almost always grooved anteriorly and inclined forwards over the body of the first vertebra to an articulation with the exoccipitals and supraoccipital; in the groove a modicum of intercalated cartilage is very generally present, more especially in young or immature specimens. The spine of the fourth vertebra is usually directed backwards and, like the succeeding spines, is generally cleft for the support of certain of the interspinous bones of the dorsal fin, but in the absence of the latter may, like its fellows, be simple and undivided (*e.g.*, *Malapterurus*). The spines which immediately succeed the foregoing may be rudimentary or obsolete (*Arius*), or well-developed and bifid; not infrequently they are either partially anchylosed or firmly articulated to one another and to their predecessors.

The transverse processes of the fourth vertebra, very frequently those of the fifth, and more rarely those belonging to the sixth vertebra (*Platystoma*), are more or less expanded and by their partial anchylosis or sutural union form on each side of the vertebral column a broad wing-like plate of bone, the anterior margin of which is strongly decurved, for the investment of the anterior and dorsal walls of the anterior chamber of the air-bladder. The transverse process of the fourth vertebra has a broad flat root, and for the rest of its extent may be simple, or, as is more usually the case, cleft more or less deeply into distinct anterior and posterior divisions, of which the former is always strongly decurved towards its distal extremity and closely applied, even if not attached, to the lateral portion of the anterior wall of the air-bladder. The anterior division is usually applied distally to the inferior limb and stem of the post-temporal, and firmly united thereto by a ligament in such a way as to afford a rigid support to the proximal portion of the pectoral girdle. The entire transverse process invariably has its origin, not from the centrum, but from the whole length of the continuous neural arch of the complex vertebra. In certain Siluroids this process becomes modified to form the singular "elastic-spring" apparatus first described by JOHANNES MÜLLER. In some of these forms (*Malapterurus, Synodontis, Pangasius*) each anterior division is almost completely separated from the posterior division, with an oblique origin from the arch of the complex vertebra, and becoming flexible and highly elastic, expands distally into an ovoid plate which is closely applied to the corresponding lateral portion of the anterior wall of the air-bladder. In others (*e.g.*, *Oxydoras* and *Auchenipterus*) the anterior division undergoes a similar modification, but the posterior division has become completely suppressed. In all such cases the modified transverse processes are provided with powerful protractor muscles, in the form of specialized portions of the dorso-lateral musculature, which have their origin on the posterior face of the skull and their insertion into the anterior surfaces of the terminal oval plates. The transverse processes of the fifth vertebra are, as a rule, but moderately expanded, although in one case (*e.g.*, *Platystoma*) they may be as greatly expanded as the preceding processes with which, in this genus, they are in sutural union anteriorly. They are often confluent at their roots with the transverse processes of the fourth vertebra, but their distal extremities are always free. Rarely are they rudimentary (*Auchenipterus*) or absent (*Oxydoras*). Like their predecessors they have their origin from the neural arch instead of from the centrum, but always at a slightly lower level than the former. The transverse processes of the sixth vertebra vary greatly in size and in degree of expansion. They may be greatly expanded and suturally united to those of the fifth vertebra (*Platystoma*), or, while of slightly greater length, may not be more expanded than the normal processes which follow them. Their origin is always from the centrum of their vertebra. Usually they carry the first pair of ribs, but in at least two genera (*Callichrous* and *Cryptopterus*) the latter are supported by the transverse processes of the fifth vertebra.

A continuous deposit of superficial bone invests the lateral surfaces of more or fewer of the anterior vertebral centra. It varies greatly in thickness as well as in extent in different Siluroids, and sometimes forms no inconsiderable portion of the otherwise somewhat attenuated anterior centra. The centra of the complex and fifth vertebra are invariably so invested; less frequently the deposit may extend on to the lateral surfaces, or at all events along the ventro-lateral margins of the sixth and seventh, or even the eighth vertebræ. The ossifications are always strongly developed along the ventro-lateral edges of the centra they invest in the form of parallel ridges, which enclose between them a deep median groove for the dorsal aorta (*e.g.*, *Macrones*). By the ventral union of these ridges the groove may become converted into a complete canal (*Arius*, *Auchenipterus*, *Platystoma*, *&c.*). Exceptionally, the dorsal aorta appears to burrow its way through a canal in the centra of the complex, the fifth, and the sixth vertebræ (*Platystoma*), a fact which in this case is apparently due to the unusual thickness of the investing superficial ossifications. The ossifications may also extend laterally on to the ventral surfaces of more or fewer of the anterior transverse processes, forming a floor for the cardinal grooves, and thereby converting the latter into complete canals (*e.g.*, *Arius*, *Batrachocephalus*, *Osteogeniosus*, *&c.*). They usually obscure the intervertebral sutures between the different vertebral centra, but sometimes (*e.g.*, *Platystoma*) the sutures are obvious externally on the surface of the investing ossifications in the form of wavy interdigitating lines.

Special developments of the system of superficial ossifications also take place in relation with the skeletal attachments of the air-bladder in the region of the complex vertebra. The anterior margins of the ossifications investing the sides of the complex centrum are thickened near the anterior extremity of the latter in the form of two more or less well-marked oblique lateral ridges, which coincide with the mesial attachment of the dorsal edge of the transverse membrane, and not infrequently, also, with the corresponding attachment of the anterior pillars of the air-bladder. An osseous nodule (radial nodule) is invariably attached to the dorsal and hinder extremity of each lateral ridge, sometimes by anchylosis, especially in old specimens, but more frequently by a firm fibrous union. These nodules coincide with the fixed attachment of the radial fibres of the tripodes. A slender lamina or spicule of bone is prolonged from the dorsal extremity of each lateral ridge, from which, however, it is often distinct, and passing obliquely backwards and outwards ventrad to the cardinal groove, extends for a varying distance on to the ventral surface of the transverse process of the fourth vertebra, and finally blends therewith. This lamina (dorsal lamina) corresponds with the dorsal attachment of the transverse membrane, and posteriorly often receives the insertion of a sheet of fibres derived from the lateral portions of the primary transverse septum of the air-bladder.

The lateral surfaces of the complex and fifth centra are almost always traversed by deep grooves which are situated between the dorsal margins of the superficial ossifications and the roots of the modified transverse processes. As a rule each groove is completely encircled by bone only in the region of the dorsal lamina, but in those cases (*e.g.*, *Arius*, *Osteogeniosus*) where the superficial ossifications extend from the sides of the complex and fifth centra on to the ventral surfaces of the transverse processes of the fourth vertebra, the groove becomes a complete canal for its whole length. The grooves transmit the posterior cardinal veins, and very generally also the attenuated anterior portions of the mesonephros as they pass forwards to join the so-called "head kidney" anteriorly. In correspondence with the unsymmetrical development of these veins, the right cardinal groove or canal is always much larger than the left.

Stout subvertebral processes are frequently developed in relation with the anterior end of the complex centrum. In some forms (*Arius* and its allies) the process is a strong conical structure apparently formed by the downward growth and coalescence of processes derived from the ventral surfaces of the basioccipital and the first and complex vertebræ, but thickened posteriorly by the superficial ossifications of the complex centrum. In others (*e.g.*, *Plotosus*) paired processes, formed apparently by an extension of bony deposit from the superficial ossifications of the complex centrum into the mesial portion of the transverse membrane, may together form a transversely-disposed, fan-shaped subvertebral process. In *Plotosus* the latter only are present, but in *Auchenoglanis* an additional pair of similar but smaller processes are developed from the ventral surface of the body of the first vertebra, and serve to buttress anteriorly the former pair. All such subvertebral processes, while partially owing their formation to an exaggerated development of the accessory articular processes which are normally present in some Siluroids (*e.g.*, *Macrones*), are, nevertheless, greatly thickened and enlarged by their association with the contiguous superficial ossifications. In all forms in which these processes are present they form a rigid support to the mesial portion of the anterior wall of the air bladder, and are usually cleft (*Auchenoglanis*) or perforated at the base (*Arius*) for the transmission of the dorsal aorta.

In the pectoral girdle the post-temporal bone always has a transversely or obliquely disposed inferior limb for articulation at its inner extremity with the lateral surface of the basioccipital, in addition to an ascending process for articulation with the pterotic and epiotic bones, and a descending process or stem for articulation with the clavicle. The socket for the clavicle is usually formed by a deep cleft in the stem, which is often more or less completely closed by the opposition of the transverse process of the fourth vertebra. Where the transverse process of the fourth vertebra fails to articulate with and support the post-temporal, as is the case in all Siluroids possessing an "elastic-spring" apparatus, the inferior limb of the latter is exceptionally massive, with an extensive articulation, or even partial anchylosis, with the basioccipital, or, in addition, with the exoccipital also. In other genera (*Macrones, Bagrus, &c.*) the inferior limb, in conjunction with the body of the same bone, may form a bony expansion or post-temporal plate, which, with the produced crescentic distal extremity of the anterior division of the transverse process of the fourth vertebra, forms a slightly concave bony structure for the support of the lateral portion of the anterior wall of the bladder. From being but faintly concave on its posterior face, the post-temporal plate and the adjacent portion of the inferior limb may become deeply excavated to form a goblet-shaped cavity, into which a thin-walled cæcal diverticulum of the air-bladder extends (*Macrones aor.*).

Where post-temporal plates are formed the sockets for the clavicles are in the form of tubular canals traversing the substance of the plates.

Apart from those which are characteristic of all Siluroids, no important modifications of the hinder part of the skull are observable in the normal members of the group, either as regards the more general features of structure, or the more special points involved in the mode of formation and relations of the "cavum sinus imparis," or of its bilobed backward prolongation, the "atria sinus imparis." The uniformity in the latter respect is so marked, that a description of those structures as they occur in any one normal Siluroid (*e.g.*, *Macrones*) will practically apply to all the others.

Of the minor variations we may remark the occasional translucency of certain of the periotic bones, such as the prootic and epiotic bones, and the opisthotic plates of the exoccipitals; the strengthening of the posterior wall of the atrial cavities by a column-like process of bone derived from the dorsal margin of the posterior face of the basioccipital, or by a slight downward growth of the posterior margin of the roof of the cavum sinus imparis, and the withdrawal of the external atrial apertures altogether within the neural canal (*e.g.*, *Aspredo*).

As regards the internal ear, the condition of many of our specimens was such that our observations were necessarily somewhat incomplete. The condition of the membranous labyrinth, and its relations to the cavum sinus imparis and to the atrial cavities, were investigated in a large number of Siluridæ normales, but with the purely negative result that we could detect no variations of any importance from the arrangement of these structures, already described for *Amiurus catus* by RAMSAY WRIGHT, and for *Silurus glanis* by WEBER, and in *Macrones* by ourselves. In all cases we found a transversely disposed ductus endolymphaticus connecting the two sacculi, and, attached to the ductus, a median pear-shaped sinus endolymphaticus projecting backwards into, and almost completely filling, the "cavum sinus imparis."

With the exception of the intercalarium, the Weberian ossicles exhibit but little variety in shape, or in their relations to one another, or to the atrial cavities and air-bladder. The variations in the condition of the tripus relate principally to the degree and shape of the curvature of its posterior or crescentic process. In some genera (*Auchenipterus*, *Oxydoras*) the "crescentic process" is almost straight; in others almost hook-shaped (*Plotosus*); and between these extremes the process may exhibit almost every degree of curvature. A ventral ridge on the root of the crescentic process, to receive the insertion of a slip of fibres from the adjacent anterior wall of the bladder, is very generally present, and varies in size according to the thickness of the walls of the bladder. In some Siluroids (*Macrones, Liocassis*) the outer convex margin of the process may be increased for the purpose of fibrous attachment, and possibly for leverage, by the addition of an outwardly directed heel-like process, which occasionally may be of considerable length (*e.g.*, *Bagroides*). The articular process of the tripus is usually distinct from the complex centrum, with which, however, it articulates at the bottom of a deep pit-like depression. It is very rare, as in the two genera *Oxydoras* and *Auchenipterus*, for the process to be flexible and elastic, and directly continuous by an oblique origin with the anterior part of the neural arch of the complex vertebra, like the adjacent and similarly elastic root of the "elastic-spring" apparatus. The proportional lengths of the anterior and crescentic processes vary somewhat in different forms; generally, the two processes are of approximately equal length, but when otherwise it is the anterior which is the longer.

The intercalarium varies greatly in development. Usually a small osseous nodule imbedded in the interossicular ligament, the intercalarium may, in addition, be prolonged therefrom as a horizontal spicule which terminates in the fibrous wall of the neural canal, between the arch of the complex vertebra and the ascending process of the scaphium, near the dorso-lateral margin of the anterior portion of the complex centrum, with which, however, it is in no way directly attached (*Cryptopterus*, *Callichrous*). In a few genera (*Macrones, Liocassis, Pseudobagrus,* &c.) the horizontal process is prolonged upwards into a vertically disposed or ascending process, which also lies in the fibrous wall of the neural canal, behind and parallel to the ascending process of the scaphium. In all cases where an ascending process is present, it lies between the paired foramina for the exit of the dorsal and ventral roots of the second and third spinal nerves.

The only variations noticed in the condition of the scaphium relate to the occasional absence of an ascending process; a globose condylar process is always present.

Claustra are invariably present, but vary greatly in size, from the usual condition of extremely slender spicules to somewhat triangular plates (*Pangasius Buchanani*).

The air-bladder has the same fundamental structure in all the S. normales. In all cases the organ is more or less cordate in shape, and is subdivided internally by a T-shaped arrangement of a primary transverse septum and a longitudinal septum into three intercommunicating compartments, of which one is anterior and transversely disposed, occupying the anterior third of the bladder, and two posterior and lateral longitudinally arranged chambers, constituting the posterior two-thirds of the bladder. The dorsal wall of the anterior chamber is closely moulded to the ventral and lateral surfaces of the complex and fifth vertebral centra, including the sub-vertebral keel which these centra form, and also to the ventral surfaces of the modified transverse processes of the fourth and fifth vertebræ. The lateral portions of the anterior wall of the chamber are also partially buttressed by the decurved anterior margins of the transverse processes of the fourth vertebra, with or without the aid of the expanded inferior processes of the post-temporals (post-temporal plates), while the median portion of the wall is not infrequently supported by a sub-vertebral process (*e.g.*, *Arius*). The lateral compartments, on the other hand, are neither invested by bone, nor are they in any way directly attached to the skeleton, but lie free in the abdominal cavity. Except in relation to the size of the Fish, the variations in the capacity of the anterior chamber as compared with those of the lateral compartments are but slight, and, as a rule, any increase or diminution in the relative size of the bladder is mainly due to variations in the size of the lateral chambers. With the exception of two genera (*Rita* and *Aspredo*) included in this group, the capacity of the anterior chamber is always much smaller than the combined capacities of the two lateral chambers, and, in one of the two exceptions referred to (*Rita*), the partial suppression of the lateral compartments is compensated by the development of two large lateral cæca from the anterior chamber. In the two genera last mentioned the lateral chambers are very small in one (*Rita*), and almost non-existent in the other (*Aspredo*), but in both cases a primary transverse septum is present, and retains its normal attachments to the skeleton. Apart from its longitudinal constriction into two laterally bulging halves—a separation which in some cases (*e.g.*, *Arius*, *Callichrous*, &c.) may be emphasised by the formation of one or two longitudinally arranged and inwardly projecting ridge-like aggregations of fibres from the median line of the posterior, ventral, and anterior walls—the cavity of the anterior chamber has smooth walls, and is not subdivided by the growth of internal septa.

The lateral compartments may also have undivided cavities (*e.g.*, *Auchenoglanis*, *Callichrous*, and *Silurus*), but not infrequently they are rendered more inexpansible, and possibly at the same time less compressible, by the formation of a variable number of secondary transverse septa (*e.g.*, *Macrones*), which incompletely subdivide each chamber into a series of transversely arranged, intercommunicating spaces. The support which these septa afford to the walls of the lateral chamber is, in some cases, strengthened by root-like bundles of fibres which grow out from the dorsal and ventral margins of the septa, and extend into the corresponding walls of these chambers. Occasionally the excessive development of these septa, and their union by root-like bundles of fibres which pass between their opposed surfaces, may lead to the formation of a thick trabecular network of fibrous columns or bands, and to the partial obliteration of the cavities of the two chambers (*Pangasius*).

The width of the primary transverse septum, forming the posterior wall of the anterior chamber, varies greatly in different Siluroids. In some (*e.g.*, *Auchenoglanis*) the septum is co-extensive with the width of the air-bladder, although contracted dorsally to admit of the lateral chambers communicating with the anterior chamber; in others (*e.g.*, *Callichrous*, *Cryptopterus*) the septum is reduced to the condition of a narrow, but stout, column-like aggregation of fibres.

In many members of this group the primary transverse septum, and more particularly its median portion, is more or less oblique, and in some extremely so. This obliquity of the septum has the effect of causing the lateral chambers and the longitudinal septum to extend forwards to a varying extent, ventrad to the inclined septum, and consequently to overlap the anterior chamber along the greater part of its ventral surface.

Cæcal appendages to the anterior and lateral compartments are not uncommon. The anterior chamber may have small anterior cæca (*Macrones aor*), or much smaller antero-lateral cæca (*Osteogeniosus*). In the former case the cæca bulge forwards into goblet-shaped cavities excavated in the substance of the inferior processes of the post-temporal bones. Lateral cæca are sometimes present, and may either take the form of large funnel-shaped structures, which extend the whole length of the abdominal cavity and are entirely free from internal subdivisions (*Rita*), or may occur as small forwardly directed outgrowths, subdivided internally by a network of fibrous bundles, and communicating with the anterior chamber by a number of slit-like orifices in its lateral walls (*Platystoma*). The lateral compartments are frequently either constricted or prolonged into a posterior cæcal appendage. This may be a longer or shorter tubular, or a slightly oval structure, and confined to the abdominal cavity (*Pangasius Buchanani*, *Bagroides melanopterus*), or a long tapering tubular structure, which, after traversing the abdomen, extends for some distance along the right side of the tail between the hæmal arches and the lateral musculature (*e.g.*, *Cryptopterus micronema* and *C. micropogon*). In some cases the posterior cæcum is very large, and in shape an elongated oval body (*Pangasius djambal*, *Malapterurus electricus*), or it may be flattened and leaf-like (*Pangasius macronema*). In one instance (*Oxydoras*) it is very rudimentary. The existence of a pair of rudimentary posterior cæca is very rare (*Auchenipterus obscurus*). Very generally the longitudinal septum extends backwards into the posterior cæcum, and subdivides its cavity into two distinct lateral canals or chambers, which communicate anteriorly with the proper lateral compartments of the bladder. Not infrequently the single or double cavity of the cæcum is partially subdivided internally by a series of circularly disposed, inwardly projecting ridges (*e.g.*, *Malapterurus*). In some Siluroids (*Pangasius*), where the lateral chambers are largely occupied by a trabecular network of fibrous bundles, the cavity of the posterior cæcum is largely obliterated by the formation of a similar growth. It may be remarked that cæcal appendages are very characteristic of those Siluroids in which an "elastic-spring" apparatus is present. They may be very rudimentary (*e.g.*, *Auchenipterus obscurus* and *Oxydoras*), but it rarely happens (*e.g.*, *Auchenipterus nodosus*) that they are completely absent. Even when present and well developed in such Siluroids, there is considerable variety in the extent to which the cavities of these appendages are sub-divided, or even partially obliterated by the growth of internal septa and fibrous trabeculæ.

Except, perhaps, in the case of *Rita*, the significance of these cæcal structures is not always obvious. This is more particularly the case with the posterior cæcal prolongations of the air-bladder, but with the antero-lateral cæca it is somewhat different, and a possible explanation of their existence may be suggested.

A branching condition of the air-bladder, with the branches ending in cæcal extremities, is very common in certain Physoclist genera,* and occasionally such branches may acquire a close relation with the internal ear. In the genera *Holocentrum* and *Sargus*, two cæcal processes are given off from the anterior end of the air-bladder, which diverge as they pass forwards, and ultimately become applied to the fibrous membranes, closing what would otherwise be vacuities in the outer walls of the auditory capsules. A similar arrangement has been described by PARKER (31) as existing in the Red Cod (*Lotella bacchus*), while WEBER (39) first recorded the existence of an analogous but more intimate connection between the two structures in the Herring (*Clupea harengus*). It may at least be conjectured that the connection between the air-bladder and the internal ear in these Fishes subserves a function similar to that of the Weberian mechanism in the Ostariophyseæ, although, no doubt, in a very primitive and rudimentary fashion, and, therefore, that these cæcal structures represent an initial stage in the evolution of that mechanism. We are not aware of the existence of antero-lateral cæca in any Ostariophyseæ but the Siluridæ. SAGEMEHL (33), however, has described the tunica externa of the air-bladder in certain Characinidæ, as being prolonged forwards in the form of a twisted ligament, which anteriorly splits into two, and is attached to the posterior portion of the base of the cranium. Although these ligaments are solid, and have no lumen, and it is expressly stated that the tunica externa has no share in their formation, SAGEMEHL regards them as the atavistic vestiges of an original and primitive connection between the air-bladder and the internal ear, which preceded the evolution of the Weberian mechanism, but is apparently still retained in some cases. The suggestion is certainly an ingenious one, but as regards the Characinidæ, we are not sure that much can be said in its favour. It is quite possible that the ligaments in question are merely illustrations of the many and various ways in which the air-bladder in the Ostariophyseæ becomes more or less intimately attached to the skeleton for physiological purposes, and, after all, may have no such significance as that suggested. On the other hand, the antero-lateral cæca of such Siluroids as *Macrones aor*, *Osteogeniosus*, and *Platystoma*, are hollow forward prolongations of the air-bladder, involving extensions of both the tunica externa and interna, and in their case SAGEMEHL's suggestion may be reasonably accepted.

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* See GÜNTHER (14, pp. 144–145; also 15).

The persistent and usually bilobed "head-kidney" usually occupies a recess of corresponding shape in relation with the anterior wall of the air-bladder, to which indeed its posterior surface is closely applied. The peritoneum invests the ventral surface of the air-bladder, and, anteriorly, extends over the corresponding surface of the "head-kidney," but at the anterior margin of the latter is reflected backwards along the dorsal surface of the œsophagus. Outwardly directed peritoneal cul-de-sacs in relation with the antero-lateral regions of the air-bladder are almost invariably developed for the reception of portions of the lateral lobes of the liver. Their formation appears to be due to the unusual lateral extension of the anterior chamber of the air-bladder, and its apposition on each side to the external skin (lateral cutaneous areas)—a modification which has led to the displacement of the lateral lobes of the liver from their normal position between the bladder and the side walls of the body, and to the outward and forward hernia-like protrusion of a portion of each lobe into special peritoneal pouches. Between the peritoneum and the proper ventral wall of the air-bladder the latter is invested by a superficial coat of connective tissue which varies in consistency and often assumes the condition of a definite fibrous membrane, more particularly where it invests the anterior wall of the bladder, in which position it forms a fairly strong, inextensible, transversely disposed, fibrous membrane, varying in thickness in different Siluroids, and specially attached to the skeleton along its dorsal edge and lateral margins. To a varying extent this superficial coat may be traced on to the lateral and dorsal walls, as well as the anterior wall of the anterior chamber, and also, but less obviously, on to the corresponding surfaces of the lateral compartments. The skeletal attachments of the transverse membrane vary somewhat in different Siluroids. Dorsally, it is always attached near the median line to the complex centrum and especially to its oblique lateral ridges, and by a special backward prolongation to the anterior margin of each dorsal lamina, and also to the anterior margins of the transverse processes of the fourth vertebra; laterally, it is firmly attached to the decurved distal extremities of the transverse processes and there blends with the ligamentous fibres by which the latter are usually connected with the post-temporals. The dorsal margin of the membrane is always more or less continuous with the fibrous floor of the saccus paravertebralis. Where an "elastic-spring" apparatus is present the membrane is continuous with the margins of the terminal plates, and from thence is continuous with the connective tissue investment of the lateral and ventral surfaces of the anterior chamber of the air-bladder. In those Siluroids in which subvertebral processes are present the transverse membrane is always attached to their lateral and ventral margins.* Anteriorly, the dorsal margin of the transverse membrane is more or less obviously continuous with an aponeurotic membrane which, after investing the dorsal surface of the "head-kidney," and the ventral surfaces of the centrum of the first vertebra and the hinder portion of the basioccipital, extends ventrally as a transversely disposed fibrous sheet in relation with the anterior surface of the "head kidney," and laterally blends with the ligamentous fibres that unite the post-temporals with the transverse processes of the fourth vertebra. This aponeurotic membrane we regard as a dorsal and backward extension of the same fibrous sheet that, ventrally, separates the pericardial and abdominal cavities. On the contrary, the connective tissue investment of the air-bladder and its special development, the transverse membrane, must be considered as belonging to that organ, of which it is really the superficial coat. These structures are of some interest for two reasons—first, because they are liable to become the seat of ossified deposit; and, secondly, because the inextensibility and the skeletal attachments of the transverse membrane enable it to supplement other structures in affording a rigid support to the anterior wall of the bladder.

In almost all normal Siluroids the lateral or outer walls of the anterior chamber of the air-bladder are more or less extensively and intimately applied to lateral cutaneous areas, and this relation of the two structures is always brought about by the divergence of the dorso-lateral and ventro-lateral muscles of the trunk combined with an unusual lateral extension of the anterior portion of the bladder.

In all the normal Siluroids, without an exception, a ductus pneumaticus is present, and, after a sigmoid or slightly tortuous course, opens into the anterior chamber in the median line of its ventral wall, and immediately in front of the ventral margin of the primary transverse septum.

The general structure of the walls of the air-bladder in all normal Siluroids is essentially similar to that we have already described in *Macrones* (p. 92), but their thickness is subject to considerable variation in different species. The fundamental arrangement of the fibres of the tunica externa in the form of an inner stratum of circularly disposed fibres and an outer stratum of longitudinal fibres is always so far departed from, that the fibres of both strata vary their course and direction in different parts of the bladder, although at any one point the fibres of one layer rarely agree in direction with those of the other, but intersect at a greater or less angle. It is only as the two strata approach their common attachments to the skeleton that their component fibres coincide in direction. The variable course of the fibres is largely due to the differentiation of special tracts of fibres in certain regions of the air-bladder for skeletal attachments.

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* In a few genera, and notably in the normal Pimelodinæ, no distinct transverse membrane exists, and in such cases it seems probable that the membrane has coalesced with the proper anterior wall of the bladder, and shares with the latter its dorsal attachment to the anterior margins of the transverse processes.

Not only is the anterior compartment of the air-bladder more or less completely invested by bone on its dorsal and anterior surfaces, but its walls are attached to rigid portions of the axial skeleton and to movable ossicles at certain special points. As to the nature and extent of the fixed skeletal attachments, there is substantial uniformity in the different members of the group, and the physiological effect of such skeletal connections is, in the great majority of cases, the same, viz., to render the anterior, dorsal, ventral, and posterior walls incapable of participating in any distension of the chamber, which, consequently, must solely depend upon the movement of the lateral walls. The posterior wall, *i.e.*, the primary transverse septum, is always attached at its dorsal margin to the ventral and lateral surfaces of either the complex or the fifth centrum—rarely to the sixth centrum; laterally to this the dorsal edge of the septum is invariably attached to the ventral surfaces of the transverse processes of the fifth vertebra, or to those of the fourth vertebra, or exceptionally to the corresponding processes of the sixth vertebra; and, in addition, a sheet of fibres is often prolonged forwards, on either side of the complex centrum, into the dorsal wall, where it eventually becomes attached to the dorsal lamina of its side. These attachments we have elsewhere referred to as the "posterior pillars" of the compartment. As the anterior wall is usually more or less efficiently buttressed by the transverse processes of the fourth vertebra, or by post-temporal plates, or median subvertebral processes, the extent of its attachment to the skeleton varies inversely with the extent to which it is invested or supported by bone. The median portion of the wall is always attached dorsally to the ventral surface and sides of the anterior portion of the complex centrum, often by means of laterally situated, oblique, bony ridges, and also to the radial nodules. Laterally to this, on each side, the anterior wall may be so completely invested by bone as to be free from any special connexion or attachment to rigid portions of the axial skeleton (*e.g.*, *Macrones*); or in correlation with a less complete bony support, the outer stratum of the tunica externa of the anterior wall may separate dorsally from the inner stratum, and become firmly inserted into the decurved anterior margin of the transverse process of the fourth vertebra (*e.g.*, *Arius*, *Auchenoglanis*, *Pimelodus*). The dorsal attachment of the median portion of the anterior wall to the radial nodules and to the complex centrum occurs in all the normal Siluroids, and may be regarded as constituting the "anterior pillars" of the compartment. The ventral wall may also be considered as rigidly attached to the skeleton, both in front and behind, inasmuch as its inner stratum of longitudinally disposed fibres, sometimes thickened into stout inwardly projecting ridges, extends into both the anterior and posterior walls, and shares the skeletal attachments of the anterior and posterior pillars.* Although, as a rule, extremely thin, the median portion of the dorsal wall, over an area bounded in front and behind by the anterior and posterior pillars, and laterally by the dorsal walls of the two outwardly bulging halves of the chamber, is always firmly attached to the ventral and lateral surfaces of the complex centrum, and possibly also to those of the fifth centrum.

The attachment of the walls of the anterior chamber to movable ossicles (the tripodes) is effected by the convergence of the fibres of both strata of the tunica externa of the anterior and lateral walls into the dorsal wall in the form of two triangular sheets, and their ultimate insertion into the crescentic processes of the tripodes, which are situated near the anterior and inner corners of the lateral halves of the anterior chamber. As pointed out in the special case of *Macrones nemurus*, it is generally also the case in most other normal Siluroids that the fibres, which at one end of their course are inserted into the movable tripodes, are at the other extremity absolutely or relatively fixed, the fibres of the inner stratum of the tunica externa being successively continued from the ossicles into the dorsal, the lateral or antero-lateral walls, and eventually into the ventral wall, and from thence into the primary transverse septum to the skeletal attachments of the latter, while the curvilinear fibres of the outer stratum follow the same course until they reach the lateral walls, from whence they are ultimately traceable into the relatively fixed or inexpansible walls of the lateral compartments. The variations in the extent to which these fibres are attached to the tripodes are mainly confined to one feature. A slip of fibres derived from the median portion of the anterior wall is always inserted dorsally into the ventral ridge of each tripus, or directly into the ventral surface of the ossicle when the ridge fails to be developed. Laterally to this point the fibres forming the whole thickness of the tunica externa of the anterior and lateral walls may converge in the dorsal wall and become attached to the tripodes (*e.g.*, *Macrones*); or as in many other Siluroids (*e.g.*, *Arius*, *Pimelodus*, &c.), the outer stratum of the anterior wall is continuously attached by its dorsal edge to the transverse process of the fourth vertebra, and only the comparatively thin inner stratum, in addition to the fibres of both strata from the lateral walls, extend into the dorsal walls and constitute the triangular sheets. In the latter case but few, if any, of the fibres of the inner stratum reach the tripodes, which, in consequence, only receive the direct insertion of the outer stratum of the tunica externa of the lateral and antero-lateral walls.

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* A further device, with the like object of giving additional rigidity to the ventral wall, may, perhaps, be found in the obliquity of the primary transverse septum, and in the tendency of the lateral compartments to more or less completely overlap the anterior chamber on its ventral side, which are such obvious features in the air-bladders of many species of *Arius* and some Pimelodinæ.

Radial fibres arising from the radial nodules and inserted into the concave inner margins of the crescentic processes of the tripodes or into the corresponding margins of their ventral ridges are invariably differentiated from the dorsal wall of the anterior chamber. In two instances (*Auchenipterus*, *Oxydoras*), where the function of the radial fibres is taken by the flexible and highly elastic articular process of the tripus, the former are but scantily and feebly developed.

As we have previously pointed out, the lateral compartments of the air-bladder are neither invested by bone nor are they directly attached to the skeleton, but project freely into the anterior portion of the abdominal cavity. The most important feature in connection with their structure, apart from their relatively greater capacity when compared with the anterior chamber, is their separation by a common longitudinal septum and the frequently septate condition of their cavities. Physiologically, the longitudinal septum and the secondary transverse septa subserve the double function of rendering the lateral chambers almost incapable of distension, and at the same time diminishing the susceptibility to the effects of external pressure. Hence it follows that all variations that may take place in the volume of the air-bladder are dependent on the lateral expansion or contraction of the anterior chamber.

Not the least remarkable feature in the air-bladder of the Siluroid Fishes is the liability of its walls to become invaded by ossified deposit, either by extension from certain of the adjacent skeletal elements which are always more or less intimately connected with the organ, or by apparently independent ossifications that subsequently coalesce with the contiguous skeletal structures. The oblique lateral ridges of the complex centrum are clearly ossifications of the transverse membrane along the line of its mesial and dorsal insertion into the lateral surfaces of the centrum. Similarly, the dorsal laminæ are to be regarded as ossifications of the dorsal portion of the superficial coat of the air-bladder. In our previous references to the skeletal attachments of the dorsal margin of the transverse membrane we described the latter as not only inserted into the lateral ridges of the complex centrum, but also as being prolonged backwards on each side of the centrum and dorsad to the anterior chamber of the bladder in the form of a slip of fibres which is ultimately inserted into the anterior margin of the dorsal lamina of its side. The direction of the dorsal lamina, as it passes from the ventral surface of the transverse process of the fourth vertebra to its junction with the lateral ridge of the complex centrum and the radial nodule, exactly coincides with the course of this strip of fibres, so that the lamina appears as an ossified backward prolongation of the latter to an original insertion into the modified transverse process. In fact, there can scarcely be any doubt that both the lateral ridges and the dorsal laminæ result from the ossification of the superficial coat of the bladder along the lines of its primitively wholly fibrous attachments to the sides of the complex centrum and to the ventral surfaces of the transverse processes of the fourth vertebra. The slightly free posterior margin of the dorsal lamina, as we have already mentioned, receives the insertion of the more laterally situated fibres of the posterior pillars which curve forwards into the dorsal wall of the anterior chamber, and it is possible that the ossification of those fibres along the line of their skeletal attachment may have somewhat widened the lamina in some Siluroids (*e.g.*, *Macrones*), but in many others (*e.g.*, *Platystoma*, *Malapterurus*, &c.), where the dorsal lamina is represented in the usual position by a very slender spicule of bone, and the lateral portions of the posterior pillars are inserted more posteriorly than in *Macrones*, that is, to the ventral surfaces of the transverse processes of the fifth vertebra, it is probable that the lamina is formed solely by the ossification of the superficial coat of the air-bladder.

There can be but little doubt that the radial nodules are independent ossifications of the tunica externa in relation with the skeletal attachments of the radially disposed fibres converging from the concavities of the crescentic processes of the tripodes towards the complex centrum, which may either permanently retain their close fibrous connection with the centrum or become anchylosed thereto. RAMSAY WRIGHT (43) has shown that the crescentic process of the tripus, or at all events the inwardly curved portion which is imbedded in the dorsal wall of the bladder, is also formed as an ossification of the tunica externa, and only secondarily becomes continuous with the remainder of the ossicle. The same writer (*loc. cit.*) refers to the superficial ossifications investing the sides of the complex and fifth vertebral centra as "developed in connection with the air-bladder." If this be so the ossifications are obviously due to the conversion into bone of the outer stratum of that part of the tunica externa of the dorsal wall of the anterior chamber which is moulded and adherent to the lateral and ventral surfaces of these centra, and the fact that the ossifications are always co-extensive with that part of the dorsal wall which is represented by little more than the tunica interna, and certainly appear to replace the tunica externa in that region, confirms this conclusion.* It would seem, therefore, a legitimate inference that these ossifications are due to the conversion into bone of the primitively more extensive, purely fibrous attachments of the posterior pillars to the lateral and ventral surfaces of the complex and fifth centra† in much the same way that the oblique lateral ridges and the dorsal laminæ are ossifications in the skeletally attached portions of the superficial coat. It may be also concluded that all such adventitious ossifications as those above mentioned are invariably formed in connection with the attachments of the bladder to fixed or movable parts of the skeleton, and that such attachments were originally wholly fibrous, but subsequently became invaded by bony deposit.

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* Recently SÖRENSEN (37) has more precisely shown that in *Platystoma* the superficial ossifications do result from the ossification of the tunica externa in the way we have suggested, and in this Siluroid may even form the greater part of the complex centrum. The same writer is of opinion that the inner layer of the peritoneum (la plèvre), or what we have referred to as the superficial coat of the bladder, is also concerned in the formation of these ossifications. As illustrating the contagious nature of this tendency to ossification, it may be mentioned that SÖRENSEN further concludes that the lateral ridges bounding the aortic groove are, in part at least, due to the ossification of the walls of the aorta itself, which may, as in *Platystoma*, even lead to the formation of a complete bony aortic canal.

† SÖRENSEN'S statement (*loc. cit.*) that in *Platystoma* the fibres in the superficial ossifications are so disposed that they exactly coincide with the direction of the fibres forming the forward extension of the posterior pillars into the dorsal wall of the anterior chamber supports this suggestion.

The post-temporal plates, which so efficiently buttress the lateral portions of the anterior wall of the anterior chamber (*e.g.*, *Macrones*, &c.) seem to have been formed by the extension of ossification from the inferior limb and stem of the post-temporal into the aponeurotic membrane and the lateral portions of the transverse membrane; and in these instances (*e.g.*, *Macrones aor*) where the wall of the bladder which is applied to these plates is exceptionally thin it is at least possible that ossification of the tunica externa has contributed to their growth.

The various subvertebral processes which probably subserve a similar function, in part, at least, owe their formation to an extension of the superficial ossifications of the complex centrum into the mesial portion of the transverse membrane.

The peculiar crescentic distal extremities of the transverse processes of the fourth vertebra, which in some Siluroids (*e.g.*, *Macrones*, *Liocassis*, *Bagrus*, &c.) partially encircle the post-temporal plates, are almost certainly formed by a similar extension of bony deposit from their proper vertebral portions into the lateral regions of the transverse membrane, the transition from the bony to the fibrous structure being readily traceable.

SÖRENSEN (*loc. cit.*) has shown that the terminal plates of the "elastic-spring" apparatus are often formed in a precisely similar fashion. In *Malapterurus* for example, he concludes that these structures are due solely to the ossification of the transverse membrane (or "la plèvre"), but in such forms as *Synodontis* and *Doras* ossification implicates the outer stratum of the tunica externa of the air-bladder as well. Our own investigations enable us to state that *Auchenipterus*, *Oxydoras*, *Pangasius djambal*, and *P. Buchanani* resemble in this respect the two last-mentioned genera, while *P. juaro* and *P. macronema*, on the contrary, agree with *Malapterurus* in that the plates are formed by the ossification of the transverse membrane alone.

The formation of bony deposits in the proper walls of the air-bladder or in its superficial coat has probably been determined by physiological considerations, and generally with the object of securing either a firm or more extensive connection of the walls of the air-bladder to adjacent fixed or movable skeletal elements, or a more effective buttressing of certain regions, and their significance from this point of view will be discussed in a future section of this paper.

Although we have never been able to detect the presence of intrinsic muscular fibres in the walls of the air-bladder, powerful extrinsic muscles are present in several Siluroids. In *Platystoma tigrinum*, *Pimelodus maculatus*, *P. ornatus*, and *Piramutana piramuta*, a powerful muscle takes origin from the posterior face of the skull, on each side of the foramen magnum, and is inserted into nearly the whole extent of the corresponding half of the ventral surface of the anterior chamber. As the contraction of these muscles must forcibly compress the anterior chamber, we have termed them the "compressor muscles" of the air-bladder. They probably occur in many other Pimelodinæ, but, so far as our investigations are concerned, are confined to that group.

The presence of compressor muscles is invariably associated with the existence of a pair of much smaller muscles which arise from the exoccipitals, and are inserted into the anterior wall of the anterior chamber of the bladder. The tendon of each muscle has its insertion into the anterior wall immediately external to the complex centrum, and the insertion coincides with the extension of a slip of fibres from the inner surface of the anterior wall to the ventral ridge and concave inner margin of the crescentic process of the tripus. As the contraction of these muscles must evidently have the effect of limiting the violent excursions of the tripodes which might otherwise take place when the anterior chamber is forcibly compressed by the contraction of its compressor muscles, we have suggested for each the name of "tensor tripodis."

An "elastic-spring" apparatus, provided with powerful protractor muscles, has already been described by JOHANNES MÜLLER as existing in the South American genera *Auchenipterus, Doras,* and *Euanemus*, and in the African Siluroids *Synodontis* and *Malapterurus.* To this list our investigations enable us to add the South American form *Oxydoras brevis,* and the East Indian species *Pangasius Buchanani, P. djambal, P. juaro,* and *P. macronema.* The absence of this mechanism in one species of *Pangasius*, viz., *P. micronema,* while present in all the remaining species of the genus that came under our notice, is an interesting and noteworthy fact.

Two points in connection with this apparatus may be noted, first, the reception of the outer margins of the tripodes into grooves between the terminal plates and their flexible and elastic roots, whereby the forcible compression of the air-bladder which follows the recoil of the plates, is prevented from imparting a too violent shock to the Weberian ossicles and the fluids of the internal ear; secondly, the geographical distribution of these fishes in which the mechanism is present, affords an additional instance of the singular and exceptional resemblances that have been noted between the South American, African, and East Indian faunas.

The extent to which those species with an "elastic-spring" mechanism differ from other S. normales is subject to some variation. Thus, in *Malapterurus, Pangasius juaro*, and *P. micronema*, the transverse process of the fourth vertebra retains both its characteristic divisions, although the anterior on each side forms an elastic spring, and the terminal oval plates of the mechanism are formed by the ossification of the transverse membrane alone. In *Pangasius djambal, P. Buchanani, Synodontis,* and *Doras* a further modification is introduced in the formation of the terminal plates from both the transverse membrane and the tunica externa, but the transverse process still retains a well-developed posterior division. Finally, *Auchenipterus* and *Oxydoras*, while agreeing with the last-mentioned Siluroids in the mode of formation of the terminal plates, differ from them in that the modified transverse process has lost all trace of a posterior division, and the corresponding process of the fifth vertebra has atrophied altogether, or is rudimentary.

The evolution of the mechanism presents no difficulty, inasmuch as the necessary factors are obvious in many Siluroids. The anterior division of the transverse process of the fourth vertebra is often flexible (*e.g.*, many Arioid genera), even while retaining its normal articular relations with the post-temporal, and in other Siluridæ (*e.g.*, *Macrones*) it not infrequently happens that the terminal portion of the process is in part formed by the ossification of the transverse membrane, while the protractor muscles can readily be regarded as derivatives from the anterior section of the dorso-lateral musculature which passes over, and is partially inserted into, the dorsal surfaces of the modified anterior transverse processes, on its way to the posterior face of the skull.

We were at one time tempted to think that the post-temporal plates of *Macrones* and the allied genera might represent a form of "elastic-spring" mechanism. Both in their relations to the anterior wall of the air-bladder and their growth as ossifications of the transverse membrane, and the outer stratum of the tunica externa, these plates resemble the terminal expansions of an "elastic-spring" apparatus, but that they have the same functional significance is extremely doubtful. There are no special muscles for their protraction, nor any arrangement for elastic recoil. Whatever power of backward or forward movement they possess must be very slight, and must depend entirely on the corresponding swing of the loosely articulated post-temporal bones in conjunction with the whole of the pectoral girdle, the mobility of which is certainly well marked in these as in many other Siluridæ. But it is extremely improbable that such pendulum-like antero-posterior movements of the pectoral girdle can have much effect on the post-temporal plates, seeing that their inner and ventral margins are closely attached by ligamentous fibres and by the dorsal edge of the transverse membrane to the crescentic distal portion of the modified transverse process. The connection is perhaps not so rigid but that it admits of a very slight forward or backward movement of the plates to an extent which in no case exceeds 1 mm., at all events in spirit preserved specimens. So slight a range of movement can scarcely be regarded as likely to produce any appreciable effect either on the air-bladder or its gaseous contents. For these reasons we prefer to consider the plates merely as bony buttresses for the purpose of effectually damping the anterior wall of the bladder; they consequently aid in restricting any movements of vibration, or expansion and contraction, solely to the lateral walls of the anterior chamber.

In addition to those genera and species that we have either been able to examine for the first time, or to revise, there are several others which, from the description of various writers, must also be referred to the Siluridæ normales; these are the genera *Hara*, *Pseudeutropius*, *Olyra*, *Chaca*, *Piratinga*, *Sorubim*, *Callophysus*, *Synodontis*, *Doras*, and certain species of *Platystoma* and *Arius*. The details given of the structure of the air-bladder in these forms are for the most part but scanty, and, as a rule, are only sufficient to enable us to infer that the organ is normally developed, although in several instances they certainly furnish additional illustrations of the polymorphic condition of the air-bladder in different Siluroids. Skeletal modifications are but seldom referred to except by MÜLLER in the case of *Synodontis*, *Euanemus*, and *Doras* where an "elastic-spring" apparatus is present, and in no instance is there any reference to those portions of the internal ear which are specially related to the Weberian mechanism.

With regard to the genera *Hara*, *Olyra*, *Pseudeutropius* (DAY, *loc. cit.*) and *Chaca* (CUV. and VAL., *loc. cit.*) nothing is known beyond the fact that the air-bladder is well developed and not enclosed by bone. *Platystoma fasciatum*, *P. coruscans*, and *Callophysus* are remarkable for the variable development of the curious cæcal appendages attached to the air-bladder. We have elsewhere described the antero-lateral cæca of *Platystoma tigrinum*, and according to JOHANNES MÜLLER (*loc. cit.*) precisely similar structures are also present in *P. fasciatum*, but in *P. coruscans* it would appear, on the same authority, that such appendages are entirely wanting. On the other hand, in *Callophysus* cæcal appendages are exceptionally well developed and form an elegant wreath surrounding the lateral margins of the bladder. In certain other Pimelodinæ these structures are entirely absent. With the exception of the Pimelodinæ the only other Siluroid known to possess such appendages is *Doras maculatus*, which, according to SÖRENSEN (*ante*, p. 165), has a fringe of branching cæcal tubules surrounding the lateral margins of the air-bladder. Among the variations in the structure of the air-bladder recorded by MÜLLER may be mentioned the transverse constriction of the organ into three intercommunicating and longitudinally arranged compartments in *Arius emphysetus*—a variation which was certainly not met with in any of the Ariinæ examined by us. In the Pimelodinæ *Piratinga filamentosa* is also said by MÜLLER to have the air-bladder divided into two sacs, lying one behind the other; both are said to be cellular, but while the anterior sac is in connection with the œsophagus by a ductus pneumaticus, the posterior one has no communication either with the œsophagus or with its fellow in front.

The presence of muscles in connection with the air-bladder is confined, so far as our experience is concerned, to the Pimelodinæ, but, according to CUVIER and VALENCIENNES (*loc. cit.*), powerful extrinsic muscles are also present in *Arius Milberti* and *A. cœlatus*. *A. Milberti* we have had no opportunity of examining, but in *A. cœlatus* there is no trace whatever of such muscles, and, as the same remark applies also to every one of the eleven species of *Arius* dissected by us, we fancy that the statement quoted is as erroneous in the case of *A. Milberti* as it certainly is with regard to *A. cœlatus*. The same writers have also described extrinsic muscles in connection with the air-bladder of *Ælurichthys Gronovii*, of which two on the ventral surface are said to be able to compress the bladder. The only species of this genus (*A. longispinis*) that we dissected assuredly had no such structures.

2. *Siluridæ Abnormales.*

Omitting for the present any reference to such extremely aberrant forms as *Hypophthalmus*, *Rhinelepis* and the various Loricaroid genera, we confine our summary of this group to the various genera and species that came directly under our notice. These are:—*Clarias, Saccobranchus, Eutropiichthys, Cryptopterus* (two species), *Ailia, Schilbichthys, Silondia, Acrochordonichthys, Akysis, Pimelodus* (two species), *Bagarius, Glyptosternum, Euclyptosternum, Callomystax*, and *Cetopsis*.

In all these forms the series of rigidly interconnected vertebræ includes only the first, the complex, and the fifth vertebræ, the sixth being almost invariably free. The rigid articulation of the anterior vertebræ with the skull is as marked in this group as in the preceding one, and is brought about by substantially similar means. The centrum of the first vertebra is usually somewhat more rudimentary than in the normal forms, and neither it, nor the basioccipital, nor the complex centrum, are ever provided with accessory articular processes. Subvertebral processes are never developed. The complex vertebra has the same general characters as in the foregoing group. The spinous processes of the third and fourth vertebræ form, as a rule, a continuous thin lamina of bone, usually articulated along its dorsal edge with the supra-occipital spine, and it but rarely happens that the spine of the fourth is cleft for the support of the first interspinous bone which, therefore, is usually supported by the bifid spine of the fifth vertebra. Superficial bony deposit may thicken the sides of the complex and fifth vertebral centra, and even invest the lateral and ventral surfaces of the first centrum, or, in addition, extend on to the basioccipital, partially or completely obscuring the various intervertebral sutures. A median groove for the dorsal aorta is generally indicated, but rarely (*e.g.*, *Pimelodus sapo*) becomes converted into a complete canal for any portion of its extent. Asymmetrically developed cardinal grooves are almost always present, but in one or two instances (*e.g.*, *Callomystax*) are absent. Dorsal laminæ and radial nodules are usually, but not invariably, present; exceptionally, the dorsal laminæ have no connection at their inner extremities with the complex centrum (*e.g.*, *Clarias, Glyptosternum*), and when this is the case the radial nodules may be absent (*e.g.*, *Glyptosternum*), or confluent with the inner extremities of the dorsal laminæ, and widely separated from the complex centrum (*e.g.*, *Clarias*).

The most characteristic of the various skeletal modifications exhibited by this group is the formation of more or less complete osseous grooves, recesses, or funnels for the partial or complete enclosure of the air-bladder. Such recesses are formed by the transverse processes of the fourth vertebra, either singly or in conjunction with those of the fifth vertebra, and vary greatly in depth, and in the extent to which they are surrounded by bone. They may be comparatively shallow and widely open on the ventral surface (*e.g.*, *Bagarius, Akysis, Acrochordonichthys*, &c.); or may take the form of deep, transversely disposed grooves, contracted distally, but somewhat expanded proximally (*e.g.*, *Pimelodus sapo*, *P. pulcher*, *Eutropiichthys*, *Schilbichthys*, &c.); or they may partake of the nature of transversely-arranged bony cylinders or funnels, open distally in the dry skeleton, closed in the fresh specimen by the lateral cutaneous areas, but otherwise with more or less complete osseous walls (*e.g.*, *Clarias*, *Saccobranchus*, *Callomystax*, *Cetopsis*, &c.). The transverse processes of the fourth vertebra always form the dorsal and anterior walls of the recesses and sometimes, in addition, the posterior wall also; rarely do they alone completely enclose tubular recesses (*Cetopsis*): more frequently the posterior walls are formed by the transverse processes of the fifth vertebra (*e.g.*, *Callomystax*, *Clarias*, &c.). Exceptionally, a slender, lateral bony outgrowth (ventral process) from each of the superficial ossifications investing the sides of the complex centrum may become attached to the ventral wall of the corresponding air-sac (*e.g.*, *Bagarius* and *Glyptosternum*), or, as in one or two instances (*e.g.*, *Clarias*), the outgrowths may be strongly developed, and form no inconsiderable portion of the ventral walls of the two osseous funnels. The formation of a horseshoe-shaped recess by the transverse processes of the fourth vertebra in conjunction with similar but more extensive, plate-like, lateral outgrowths from the superficial ossifications, which is open laterally and behind in the dry skeleton, occurs in one genus only (*e.g.*, *Ailia*). When not completed ventrally by bone the recesses are usually closed by a tough fibrous membrane which also invests the corresponding walls of the contained air-sacs (*e.g.*, *Bagarius*, *Glyptosternum*, and many others). This membrane we regard as the result of a special development of the superficial connective tissue which in all normal Siluridæ invests the external surface of the air-bladder, and is continuous anteriorly with the transverse membrane. In whatever way the osseous capsules or recesses may be formed they are almost always closed laterally by the external skin (lateral cutaneous areas), never, as in the more aberrant Loricaroid genera, by the post-temporals.

In none of the genera examined by us was the encapsulation of the air-bladder by bone effected wholly or in part by the actual ossification of its *proper* wall, or tunica externa, although such instances do occur in other S. abnormales (*e.g.*, *Hypophthalmus*, and probably *Acanthicus*), and in several Cyprinidæ (*e.g.*, *Cobitis*). In *Callomystax* it is probable that the ventral walls of the osseous funnels are in part formed by the extension of ossification from the decurved anterior margins of the transverse processes of the fourth vertebra into the fibrous sheet which often closes the ventral openings of the recesses, and it is also possible that in many other S. abnormales the exceptional width and downward curvature of the margins of these processes are due to the same cause. The lamellar outgrowths which form the ventral walls of the horseshoe-shaped recesses in *Ailia* are also probably due to an extension of ossification from the superficial bony deposit on the surface of the complex centrum into the same fibrous membrane; and a similar origin may possibly be ascribed to the ventral processes of *Clarias*,* *Glyptosternum*, and *Bagarius*.

As a rule the post-temporal retains its normal relations to the skull and to the transverse process of the fourth vertebra. The anterior wall of each bony recess for the air-bladder articulates at its distal end with the post-temporal stem, and frequently also along its anterior face with the inferior limb of the same bone (*e.g.*, *Glyptosternum*) ; sometimes the inferior limb is extremely slender (*e.g.*, *Bagarius*); exceptionally, it becomes quite rudimentary and loses its usual articulation with the basi-occipital (*e.g.*, *Clarias.*).

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* See also SÖRENSEN (37).

The skull presents no special modifications in any of the fifteen genera above mentioned. Whatever changes the membranous labyrinth of the internal ear may undergo, the mode of formation and the relations of the cavum sinus imparis, the atria sinus imparis, and the recesses for the sacculi are essentially the same as in the Siluridæ normales.

The condition of the air-bladder in this group is singularly varied, and in proportion to the size of the fish is always small and often diminutive. Many of its more characteristic features are clearly the results of atrophy and degeneration. The principal modifications appear to be due to the partial or complete suppression of the lateral chambers, and the partial or complete subdivision of the anterior chamber into two laterally situated cavities or air-sacs, either by the solidification of the mesial portion of the bladder, or by more or less complete longitudinal constriction. In all cases the atrophied bladder is partially or completely enclosed within bony recesses. In one or two instances (*e.g.*, *Schilbichthys*, and probably also *Eutropiichthys*) the air-bladder, although solid mesially, nevertheless retains in each half traces of its original and normal division into anterior and lateral compartments, but the extreme thickness of its walls, and the small size of its internal cavities, afford sufficient proof of its degenerate and functionless condition. Solidification of the central portion of the bladder in one instance (*e.g.*, *Silondia*) has reduced the cavity of the organ to the condition of a circular canal surrounding a massive central pillar. Two species furnish examples of the extreme variability to which degenerate structures are liable. In one (*Ailia*) the air-bladder assumes the shape of a cylindrical horse-shoe, and is almost solid through the development of internal fibrous trabeculæ, except at its hollow forwardly-curved cornua; in the other (*Pimelodus sapo*) the organ is almost solid mesially, or at all events its original cavity is obliterated by the growth of a dense fibrous network, and of its two pairs of forwardly directed prolongations one only is hollow and receives the insertion of the tripodes. In another instance (*Cryptopterus micropus*, and possibly also *C. hexapterus*) the air-bladder consists of two partially separated lateral halves, but its degenerate character is betrayed by the partial obliteration of the cavities of the greatly reduced lateral compartments by a dense network of fibrous bundles. Such facts suggest that the partial obliteration of portions of the internal cavity of the bladder, and more especially the lateral chambers, by the development therein of anastomosing fibrous trabeculæ, often precedes their more complete suppression. But despite such exceptional variations in particular species or genera, the more frequent condition of the air-bladder in this group is in the form of two simple, pyriform or globose, thin-walled, laterally placed air-sacs, which are either distinct or connected by an intermediate tubular portion (*e.g.*, *Glyptosternum*, *Euclyptosternum*, *Cetopsis*, *Bagarius*, *Akysis*, *Acrochordonichthys*, *Clarias*, *Saccobranchus*, and *Pimelodus pulcher*).

The skeletal attachments of the air-bladder to rigid portions of the skeleton exhibit as a rule much the same extent and kind of variation as we have already described in the case of the anterior chamber of the more normal Siluroids. In such forms as possess rudiments of lateral chambers, and of primary transverse and longitudinal septa, the attachments of the air-bladder to the anterior vertebræ are perfectly normal, and even in many genera where those structures are entirely wanting the skeletal attachments are often very similar to those of the normal Siluridæ. Thus in those cases in which the bladder is represented by two distinct or mesially intercommunicating air-sacs, the dorsal attachment of the primary transverse septum in the normal organ is represented either by the attachment of the dorsal edge of the median portion of the posterior wall to the ventral surface and sides of the complex centrum (*e.g.*, *Pimelodus pulcher*), or by a similar attachment of the corresponding margin of the posterior wall of each lateral air-sac to the hinder margin of the transverse process of the fourth vertebra, or to the ventral surface of the corresponding process of the fifth vertebra in those cases in which the latter process participates in the formation of the osseous recesses (*e.g.*, *Bagarius*, *Clarias*, *Glyptosternum*, &c.). The median and tubular portion of the air-bladder, when present, is always thin-walled, and its firm connection with the ventral surface of the complex centrum evidently corresponds to the skeletal attachment of the thin medio-dorsal portion of a normal anterior chamber (*e.g.*, *Clarias*). The same remark will apply also to such cases in which the median portion of the constricted air-bladder is represented by a band of fibrous tissue, without any lumen, passing from one air-sac to the other, and firmly attached to the ventral surface of the complex centrum (*e.g.*, *Bagarius*, *Glyptosternum*, and others). Whether the median tubular portion of the air-bladder be present or absent, the inner portion of the anterior wall of each air-sac is almost invariably attached to the contiguous lateral surfaces of the complex centrum, or to the radial nodule, or even to both, after the fashion of the anterior pillars of the normal bladder. Occasionally also, as in such normal forms as *Arius* and its allies, the outer stratum of the anterior wall of each air-sac may be dorsally connected with the decurved anterior margin of the transverse process of the fourth vertebra (*e.g.*, *Bagarius*, *Glyptosternum*, and *Akysis*). As a rule, however, in the limited number of instances where the air-bladder is almost completely surrounded by its osseous capsules, the rigid skeletal attachments of the former are not so obvious as in those cases in which the bony investment is but partial (*e.g.*, *Callomystax*, *Cetopsis*, &c.). Broadly speaking it may be affirmed that reduction in the size of the air-bladder, and its structural degeneration in other respects, do not to any great extent affect its normal attachments to rigid portions of the axial skeleton, except in certain instances where encapsulation by bone is more complete than is usually the case.

In addition to considerable variations in the thickness of its walls, the relations of the air-bladder to the Weberian ossicles are subject to important variations in different genera and species.

In certain genera (*e.g.*, *Bagarius*, *Glyptosternum*, *Euclyptosternum*, *Akysis*, and *Acrochordonichthys*) the dorsal wall of each air-sac has so far degenerated that it is extremely improbable that the few scattered fibres that alone remain can exert any influence on the tripus during the distension or contraction of the bladder. In most of the remaining genera, however much they may be modified in other respects, the walls of the air-bladder are structurally complete, and the convergence of the fibres forming the antero-lateral, lateral and dorsal walls of each air-sac to their insertion into the crescentic process of the tripus takes place in much the same way as in the normal Siluridæ. There would seem, however, to be some definite relation between the extent to which the air-bladder retains its structural integrity, and its apparently functional connection with the tripodes, and the extent to which it is encapsuled by bone. When the dorsal walls of the air-sacs have undergone more or less complete degeneration, and have wholly or largely lost their normal attachments to the tripodes, the air-bladder is but slightly enclosed within comparatively shallow recesses or grooves on the ventral surfaces of the transverse processes of the fourth and fifth vertebræ. The partial encapsulation in such cases may be simply due to the fact that reduction in the size of the only portion of the air-bladder that persists, viz., the anterior chamber, has been accompanied by a corresponding contraction and curvature of the modified transverse processes, which are normally moulded to the convexity of its anterior and dorsal surfaces. On the contrary, in nearly all cases in which the air-bladder retains much of its structural integrity, and, at the same time, its anatomical connection with the tripodes, it is always more completely encapsuled by bone than when the contrary is the case (*e.g.*, *Callomystax*, *Cetopsis*, and *Clarias*). In such instances, the reduced air-bladder is either enclosed within deep groove-like recesses with greatly contracted outer or distal extremities, or within tubular or funnel-like cavities almost completely surrounded by bone, and the encapsulation always seems to be more complete than can be accounted for by the mere contraction of the associated skeletal elements round an atrophying air-bladder.

Notwithstanding the reduced condition of the air-bladder, the Weberian ossicles almost always retain their normal size relatively to that of the Fish, but the comparatively slight modifications which they present in other respects are invariably in the direction of degeneration. Claustra are occasionally absent, and even when present are but very feebly developed spicules of bone. As a rule, the scaphium has no ascending process, but only spatulate and condylar processes. The intercalarium may be absent (*e.g.*, *Clarias*), in which case the interossicular ligament is extremely short, or is represented by a very small bony nodule in the usual position; horizontal and ascending processes are invariably wanting. As regards its position, the relations of the crescentic process of the tripus to each lateral air-sac are precisely similar to those of the same structure in each half of the anterior chamber in a normal Siluroid, but in shape it is variously modified. Very rarely does it retain its characteristic sickle-like form, more frequently it is nearly straight, with a pointed distal extremity (*e.g.*, *Bagarius*), or but slightly curved (*e g.*, *Glyptosternum*); exceptionally (*e.g.*, *Clarias*), the crescentic process is curiously angulated and heeled. A ventral ridge is rarely present—a fact which must be associated with the general thinness of the walls of the air-bladder, and the occasional degeneration of those fibres which normally converge from the dorsal wall and are inserted into it. The articular process of the tripus is usually long and tapering, with a pointed distal extremity, and retains its usual relations with the anterior portion of the complex centrum. The anterior process presents no special characters. Radial fibres can generally be detected, but in some cases are less obviously specialized than in others, and, where radial nodules are absent, pass directly from the lateral surfaces of the complex centrum to the inner or faintly concave margins of the crescentic processes of the tripodes. On the other hand, in those Siluroids in which the dorsal walls of the air-sacs have degenerated, radial fibres, if present at all, are very feebly developed (*e.g.*, *Bagarius*, &c.).

Lateral cutaneous areas are almost invariably well marked, and, as a rule, close the distal openings of the osseous recesses in which the air-bladder is lodged, but their relation to the outer walls of the latter vary considerably. In some forms the two structures are in close contact (*e.g.*, *Clarias*, *Callomystax*), but more frequently they are separated by a considerable interval, which is usually occupied by the lateral lobes of the liver, or even, in addition, by the mesonephros or its anterior lymphoid portion —the "head-kidney."

A ductus pneumaticus may be present or absent. It is usually present when the laterally-situated air-sacs are connected by an intermediate tubular portion (*e.g.*, *Clarias*, *Saccobranchus*, and others), but it is absent when the two sacs are completely separated or connected only by a solid fibrous band (*e.g.*, *Bagarius* and *Glyptosternum*). Rarely is it represented by a solid fibrous cord.

Our investigations into the structure of the auditory organ in this section of the family are not so complete as we could desire, and our regret is the greater because it would have been extremely interesting to ascertain how far the atrophy and degeneration of the air-bladder is correlated with similar retrogressive changes in those portions of the membranous labyrinth which are functionally related in the Weberian mechanism. That our specimens were not sufficiently well preserved to admit of accurate research on this point, is due to the fact that many of them had been preserved for some considerable time without being previously opened to secure the proper permeation of the specimens by the preservative fluids. In some genera (*e.g.*, *Bagarius*, *Glyptosternum*, *Euclyptosternum*, *Acrochordonichthys*, and *Akysis*) we entertain but little doubt that degeneration of the air-bladder *is* accompanied by corresponding retrogressive changes in the auditory organ, to the extent at least of the atrophy of the sinus endolymphaticus, although the ductus endolymphaticus still persists as a channel of communication between the two sacculi. We are also of opinion that the sinus is similarly wanting in other Siluridæ abnormales—as, for example, in *Pimelodus sapo*; but, for reasons already stated, we hesitate to speak decisively in this as well as in some other instances about which we entertain a similar belief. On the other hand, there are several genera of which we entertain no doubt as to the presence of a sinus endolymphaticus, but in which the membranous labyrinth appears to be in every respect essentially similar to that of the more normal Siluridæ (*e.g.*, *Clarias, Saccobranchus, Pimelodus pulcher*, &c.). It may be affirmed, therefore, that, while in some instances the membranous labyrinth would seem to have retained its normal structure, there are certainly other cases in which degeneration of the air-bladder has been accompanied by a corresponding simplification of those portions of the internal ear which are normally brought into physiological relation with it through the medium of the Weberian ossicles.

In addition to the Siluridæ abnormales already mentioned as forming the special subjects of our investigations, there are several other genera which, on the authority of various writers, must be referred to the same series.

Thus, on the authority of DAY (9), the Indian genera *Sisor*, *Amblyceps*, *Pseudechencis*, and *Exostoma* are Siluroids in which the air-bladder is diminutive and bone-encapsuled—a conclusion which is in harmony with their hilly habitat and Loach-like form.

JOHANNES MÜLLER's references (*loc. cit.*) to the air-bladder of the South American Siluroid *Ageniosus militaris*, and of *Heterobranchus*, warrant a similar conclusion with regard to these genera.

On the authority of REISSNER (*loc. cit.*), the following genera belonging to GÜNTHER's group Hypostomatina, viz., *Loricaria*, *Plecostomus*, *Callichthys*, and *Acanthicus*, must also be regarded as S. abnormales, and, as the genera *Arges* and *Brontes* are but the naked allies of these cuirassed Loricaroid forms, it is extremely probable that they must also be added.

According to SAGEMEHL (*loc. cit.*) the Hypostomatous genus *Trichomycterus* also possesses a diminutive air-bladder encapsuled by bone, and as *Eremophilus* is a near ally it may be conjectured that its air-bladder is in a similar condition.

Finally, it has been proved by RAMSAY WRIGHT (44) that in *Hypophthalmus* the air-bladder is degenerate and bone-encapsuled.

It follows, therefore, that in addition to the thirteen genera which we have been able to revise, there must also be included twelve others, and with some probability the three genera, *Arges*, *Brontes*, and *Eremophilus*. So that of the 116 genera enumerated in the British Museum catalogue of the family, certainly twenty-five, and probably twenty-eight, are referable to the S. abnormales. In these totals we have not included the genera *Pimelodus* and *Cryptopterus* in which only two or three species are at present known to possess degenerate air-bladders.

In certain of the preceding genera the condition and relations of the air-bladder, and the character of the correlated skeletal modifications, are sufficiently well known to admit of comparison with those dissected by us. Such a comparison clearly proves that many of the former exhibit structural modifications of an extremely interesting character. On the other hand there are others of which scarcely anything is known beyond the bare fact that the bladder is more or less rudimentary and encapsuled by bone, and no data are available for comparison with other and better known types.

Of the Hypostomatinæ about which any reliable evidence exists as to the structure and relations of the air-bladder and Weberian mechanism, we may first of all refer to a series of genera which in future we shall term the Loricaroid types; under this head we include *Loricaria*, *Plecostomus*, and *Callichthys*. There are certain points with regard to these types which are still obscure, and more particularly the structure of that portion of the internal ear which is specially related to the Weberian mechanism, but certain facts may, nevertheless, be mentioned as affording a basis for comparison, on the one hand, with such S. abnormales as we have been able to examine, and on the other, with such extremely modified forms as *Acanthicus* and *Hypophthalmus*.

From Reissner's observations on *Loricaria*, *Plecostomus*, and *Callichthys*, and from certain facts which our own investigations have enabled us to add, it may be inferred that in all these types an air-bladder is present in the form of two laterally situated sacs with structurally complete, but extremely thin walls, and connected by an intermediate narrow tubular portion, supported in *Callichthys* and *Plecostomus*, and possibly in *Loricaria* also, by an arch-shaped spicule of bone, similar to what Reissner has termed the "processus bijugus" in *Acanthicus*. So far as *Plecostomus* is concerned we could detect no trace of a ductus pneumaticus, and of the remaining genera our limited material was too badly preserved to admit of the point being determined. The air-sacs are completely enclosed within osseous capsules formed by the so-called dorsal and ventral laminæ of the transverse processes of the fourth vertebra, precisely as described by Ramsay Wright in the case of *Hypophthalmus*, and the lateral or distal apertures of the two capsules are almost completely closed by the post-temporals. All the anterior vertebræ in front of the fifth, with, perhaps, the exception of the centrum of the first which may be absent, are indistinguishably anchylosed into a "complex" vertebra,* which in turn is firmly attached, if not actually anchylosed, to the posterior face of the skull. From the mode of articulation of the complex centrum with the basioccipital, it may be concluded, that, with the possible exception of *Callichthys*, nothing comparable to the singular forward dislocation of the coalesced anterior vertebræ, which is so characteristic of *Hypophthalmus*, has taken place in these Siluroids. But little is certainly known as to the structure of the auditory organ, but it is clear that the two sacculi are closely apposed in the median line, and occupy two shallow depressions, separated by a faint median ridge, on the cranial surface of the basioccipital. The sacculi may have a fibrous investment dorsally, but it is certain that they are not roofed over by horizontal ingrowths from the exoccipitals as is the case with all the other S. abnormales that we dissected. It is also due to the absence of such ingrowths that, with the possible exception of *Callichthys*, the walls of the cavum sinus imparis are everywhere fibrous, except where it rests on the dorsal surface of the basioccipital. Whether a sinus endolymphaticus is present or absent has not yet been determined, but its presence in *Acanthicus* suggests that it may also be present here. The Weberian ossicles are very similar to those of other Siluridæ abnormales. The scaphium is a small concavo-convex ossicle without ascending or condylar processes, and lies altogether within the neural canal. The intercalarium is absent. The tripus has but a slightly curved crescentic process for insertion into the wall of the corresponding air-sac. No mention of claustra is made by REISSNER, nor could we detect any trace of these ossicles.

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* From Sörensen's account (37) of *Plecostomus*, it is possible that even the fifth vertebra may be included.

From this brief summary it is obvious that the Loricaroid types are in many respects widely different from those S. abnormales that came more directly under our notice, and exhibit a combination of characters in common which no doubt represents a further and more extreme modification of the type of structure exhibited by the latter. From this point of view the most important of the Loricaroid features are, (1.) the absence of a distinct separable centrum to the first vertebra. In all other Ostariophyseæ this centrum can be readily recognized, although in the Siluridæ it may be much smaller than any of the adjacent normal centra; but in the Loricaroid genera it has either undergone complete suppression, or has fused behind with the complex vertebra. (2.) The mode of formation of the osseous capsules for the air-bladder by what have hitherto been described as the dorsal and ventral laminæ of the transverse processes of the fourth vertebra, and by the bones forming the posterior face of the skull. It is by no means improbable that this method is partly the direct result of the reduction in size and concrescence of the anterior vertebræ, and the close relation of the modified transverse processes to the skull which is thus brought about, and partly to the further extension of a modification already indicated in other and less aberrant Siluridæ. The so-called "dorsal lamina" of the modified transverse processes in the Loricaroid forms, is clearly the equivalent of the entire process in a normal Siluroid, and like the latter has its origin from the neural arch of its vertebra. The downgrowth of the lamina to buttress the front wall of the air-bladder as in other abnormal Siluridæ is here unnecessary, inasmuch as the close relation of the bladder to the posterior face of the skull enabled the latter to be utilized in forming the anterior wall of the investing bony capsule. The so-called ventral lamina is probably to be regarded not as a portion of the transverse process as described by RAMSAY WRIGHT, but rather as a further development of the peculiar outgrowth from the superficial ossification investing the lateral surfaces of the complex centrum, which, as a rudiment, is apparent in *Glyptosternum* and *Bagarius*, but is more extensively developed in *Clarias* and *Ailia*. A special development of this process ("ventral process") and the union of its posterior margin with the corresponding edge of the modified transverse process, while the anterior margins of both remain distinct from each other but blend with the posterior face of the skull, would eventually lead to the enclosure of the air-bladder within bony capsules exactly similar to those of the Loricaroid Siluridæ.* This explanation renders necessary the assumption that the modified transverse processes of the fourth vertebra have each a double origin from the vertebra in these Siluroids, and, moreover, explains the formation of their osseous capsules as being due to the further extension of a modification already initiated in other and less aberrant S. abnormales. (3.) The imperfect closure of the saccular recesses and the cavum sinus imparis by bone. The deficiencies of the Loricaroid forms in this respect must be regarded as due to the atrophy of the horizontal plates of the exoccipitals by which these cavities are usually roofed. A transitional stage in this process is apparently represented in *Hypophthalmus*. (4.) The suppression of the intercalaria and claustra. Although a constant character in those Loricaroid forms that have yet been examined, the absence of one, or even both, of these elements is not unknown in the less abnormal members of this section of the family.

The Hypostomatous genus *Acanthicus*, while in some respects resembling *Loricaria* and its allies, in others exhibits certain characteristic features of its own. In common with the preceding forms, the air-bladder is longitudinally constricted into two laterally situated oval sacs with structurally continuous walls, and connected by an intermediate tubular portion which, as in several of the Loricaroid genera, is supported by a "processus bijugus." The presence of a ductus pneumaticus is uncertain. Each air sac is completely enclosed within an osseous capsule of corresponding shape, and, for a part of its extent, is situated dorsad to the first pair of ribs. What share the modified transverse processes take in the enclosure of the air-sacs is not clear from REISSNER's account, but the shape and smooth rounded contour of the capsules certainly suggest that they are mainly, if not exclusively, formed by the ossification of the outer stratum of the tunica externa of the air-bladder itself, and that, unlike *Loricaria*, *Callichthys*, &c., and *Hypophthalmus* the transverse processes can have but little share in their formation—a conclusion which receives some additional support from the fact that the bladder is everywhere in close contact with its bony investment, and connected therewith by fibres passing from one to the other. REISSNER seems to compare the "processus auricularis" with the distal extremity of a modified transverse process, which in *Acanthicus*, as in the Cyprinoid *Cobitis fossilis*, is perforated by certain apertures through which the external skin is prolonged inwards and attached to the outer walls of the air-bladder; but it may also be the case that the "processus auricularis" is really the post-temporal, which here, as in the Loricaroid types, closes what, in the dry skeleton, would otherwise be an aperture leading into the corresponding osseous capsule. It is difficult to judge from REISSNER'S description how far coalescence has affected the anterior vertebræ, and whether any forward dislocation has taken place. His "first" vertebra, as we have pointed out (p. 178), is probably a "complex," which may include the first to the fifth vertebræ, inclusive, but there is also the alternative that the vertebra has the same value as an ordinary "complex" in most other Siluridæ, although the possibility that the centrum of the first vertebra may also be included in it cannot altogether be left out of sight. We are of opinion that REISSNER'S "first" vertebra will ultimately be found to possess the same significance as in *Loricaria* and its allies, but a careful re-examination of this curious Siluroid is necessary before perfectly trustworthy conclusions can be arrived at. The cavum sinus imparis, the atrial cavities, and the sinus endolymphaticus are apparently normal so far as their mutual relations are concerned, and lie on the upper surfaces of the basioccipital and the anterior portion of the "first" vertebra. The relations of the scaphia to the lateral walls of the two atria would also seem to be normal. The dorsal wall of the cavum sinus imparis, however, must be fibrous, or at all events the cavum is not roofed in by horizontal plates from the exoccipitals; and in the fact that the sacculi occupy mere depressions in the cranial surface of the basioccipital, and are not surrounded by almost complete osseous capsules, *Acanthicus* also differs from *Hypophthalmus* and most other abnormal Siluridæ, and resembles the Loricaroid types. The relative positions of the sacculi, the cavum sinus imparis, the sinus endolymphaticus, and the atrial cavities almost negative the possibility of any forward dislocation of the anterior vertebræ into the cranial cavity having taken place. Claustra and intercalaria are probably absent, or at all events are neither figured nor mentioned by REISSNER. The scaphium, as in some other S. abnormales and in the Loricaroid genera, has neither condylar nor ascending processes, and, as is the case with the great majority of the abnormal types, the tripus has a straight or but very slightly curved "crescentic" process.

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* See also SÖRENSEN's account of *Plecostomus* (37).

From this summary of the more salient features in the structure of its air-bladder and Weberian mechanism, it is clear that as regards the condition and mutual relations of the cavum sinus imparis, the atrial cavities, and the saccular recesses, the existence of a "processus bijugus," and possibly also in the relations of the anterior vertebræ to the skull, *Acanthicus* closely resembles the Loricaroid genera and differs from *Hypophthalmus*. In the mode of formation of the osseous capsules for the air-sacs, however, *Acanthicus*, while peculiar among the Siluridæ, distinctly resembles, as REISSNER suggests, the Cyprinoid *Cobitis fossilis*. On the other hand, the peculiar position of the posterior halves of the two air-sacs and their bony capsules, dorsad to the first pair of ribs in *Acanthicus*, has no parallel in any known Ostariophyseæ.

The last of these extremely aberrant Siluroids, *Hypophthalmus*, exhibits an extreme type of modification, of which the most noteworthy features are the complete fusion of the first four vertebræ with one another and their partial coalescence with the fifth, and the telescoping of the three anterior vertebræ and the associated portions of the Weberian mechanism through the foramen magnum on to the upper surface of the basioccipital, so that all these structures lie wholly within the cranial cavity and dorsad to the osseous recesses for the sacculi which here, as in the normal Siluridæ, are roofed over by horizontal plates developed from the exoccipitals. With such singular modifications must also be mentioned the almost complete anchylosis of the conjoined and dislocated anterior vertebræ with the occipital portion of the skull, and the enclosure of the two completely separated air-sacs into which the air-bladder is divided within recesses formed by the so-called dorsal and ventral laminæ of the modified transverse processes above, behind, and below, and by the posterior face of the skull in front, while the lateral or distal apertures of the recesses are closed by the lateral cutaneous areas only, the post-temporals merely forming their anterior and ventral lips. The absence of a sinus endolymphaticus, although the ductus endolymphaticus still remains, the partially fibrous condition of the roof of the cavum sinus imparis, and the fact that, as a consequence of the forward dislocation of the anterior vertebræ, the scaphia form the side walls of the cavum sinus imparis instead of those of the atrial cavities, are also noteworthy features. Finally, may be mentioned the absence of a ductus pneumaticus, the partial ossification of the tunica externa of the inner half of each air-sac, and the fusion of the osseous cups so formed with the side walls of the neural canal in this region, and the presence of intercalaria and rudimentary claustra, in addition to a concavo-convex scaphium without condylar or ascending processes.

The condition of the air-bladder, Weberian mechanism and the associated skeletal structures in *Hypophthalmus* are such as to justify the conclusion that in this genus the structures in question, while in some respects more normal than in any of the Hypostomatinæ at present examined, in others reach their extreme of retrogressive modification. In the relations of the post-temporals to the skull, to the pectoral girdle, and to the modified transverse processes, as well as in the fact that they do not close the external apertures of the osseous recesses for the air-sacs, *Hypophthalmus* closely resembles the less modified Siluridæ abnormales. A further resemblance to the latter is also shown by the enclosure of the two sacculi within bony recesses formed by the basioccipital and by horizontal plates derived from the exoccipitals, the partial roofing in by bone of the cavum sinus imparis, and the presence of intercalaria and claustra. The complete separation of the two air-sacs, the atrophy of the ductus pneumaticus, and the possible suppression of the sinus endolymphaticus, may also be paralleled by similar retrogressive modifications in such otherwise less abnormal genera as *Bagarius*, *Glyptosternum*, &c. The mode of formation of the osseous capsules for the air-sacs is almost identical with the means employed for the same object in the Loricaroid genera. On the contrary, in the remarkable structural modifications involved in the forward dislocation of the anterior vertebræ and the associated portions of the Weberian mechanism into the cranial cavity, and in the combination of a partially ossified air-bladder with external osseous capsules, *Hypophthalmus* is unique among all S. abnormales which have so far been described, and represents the extreme of a series of modifications of which *Loricaria* and its allies exhibit the initial stages.*

From the facts above-mentioned it may be concluded: (1) That the Hypostomatinæ and Hypophthalminæ exhibit the most extreme modifications which the air-bladder, Weberian mechanism and the correlated skeletal elements undergo in the Siluridæ. (2) That the modifications in question have to some extent taken place in the same direction, so that the two groups possess certain features in common, and, notably, the firm sutural union, or even partial anchylosis of the anterior vertebræ with the skull, and also, with one exception (*Acanthicus*), in the mode in which the osseous capsules for the air-bladder are formed; in the partial or complete atrophy of the bony roof of the cavum sinus imparis; and in certain other features which the two groups share with the less aberrant Siluridæ abnormales. (3) That the exceptional features so characteristic of certain genera, viz., the formation of complete bony capsules for the air-bladder by the actual ossification of its own walls in *Acanthicus*, and the peculiar relation of both to the first pair of ribs; and the singular dislocation of the anterior vertebræ in *Hypophthalmus*, are sufficient to prove that very striking variations may occur within the limits of the two groups.

A careful investigation of the remaining genera of the Hypostomatinæ may bring to light other forms, some of which may prove to be even more, and others less, aberrant than those already known.

We have had no opportunity of dissecting the Indian genera, *Sisor*, *Exostoma*, and *Pseudecheneis*, which are the only Hypostomatinæ that are not restricted to South America. Some doubt has been thrown on the correctness of their presumed relationship to this group, but the mode of formation of the osseous capsules for the air-bladder, and the extent of coalescence among the anterior vertebræ, should furnish decisive evidence on this point. It is unfortunate, therefore, that the only evidence available through DAY's descriptions is confined to the bare fact that the air-bladder consists of two lateral sacs enclosed within bony capsules, no information being given about the special features so necessary for comparison with undoubted Hypostomatinæ.

The singular air-bladder of *Ageniosus militaris* (MÜLLER, *loc. cit.*) bears a remarkable resemblance to that of such Cyprinidæ as *Cobitis* and *Botia*. Not only is the organ encapsuled by bone, but the capsules are perforated posteriorly for the passage of two cæcal diverticula.

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* As RAMSAY WRIGHT (44) points out, *Hypophthalmus* occupies a somewhat isolated position among Siluroids. GÜNTHER (15) forms for the genus a distinct sub-family. COPE (7) regards the genus as the type of one of the three families into which he divides the Nematognathi (= Siluridæ); and, finally, GILL (13) reserves for it one of his eleven families of Nematognathi.

The Homology of the Weberian Ossicles.

Except with regard to the intercalarium, our investigations throw no additional light on the nature of the Weberian ossicles, and that this is the case is mainly due to the highly specialized character of this mechanism in the Siluridæ. As far as this family is concerned comparative anatomy is of but little use in the discussion of this question, and embryology is the only line of investigation which offers any prospect of a satisfactory and final solution of the problem. The views of different investigators on this point are mainly based on a comparative examination of the condition and relations of the ossicles in the less highly specialized Ostariophyseæ, and principally in the Cyprinidæ. The conclusions of **Ramsay Wright** and **Grassi**, however, rest on the development of these structures in *Amiurus catus* (Siluridæ) and the Carp (Cyprinidæ) respectively. The different views may be briefly stated in the following table :—

	Claustrum.	Scaphium.	Intercalarium.	Tripus.
Baudelot (1868) . . .	Neural spine, or divided intercrural bone of $v.^1$	Neural arch of $v.^1$	Neural arch of $v.^2$	Transverse process or rib of $v.^3$
Nusbaum (1881) . . .	Neural spine of $v.^1$	„ „	„ „	Rib of $v.^3$
Grassi (1882)	Part of the skull .	„ „	„ „	Transverse process of $v.^3$
Ramsay Wright (1884).	Neural spine of $v.^1$	„ „	„ „	„ „
Sagemehl (1885) . . .	Part of the occipital segment of the skull	„ „	Rib of $v.^2$ . . .	Rib of $v.^3$
Sörensen (1890) . . .	Neural spine of $v.^1$	„ „	Neural arch of $v.^2$	„

($v.^1$, $v.^2$, $v.^3$ = the first, second, and third vertebræ.)

The identification of the intercalarium as the neural arch of the second vertebra rests mainly on its condition and relations in certain Cyprinidæ. In *Cyprinus* the ossicle consists of an articular process which rests on the body of the second vertebra, of an ascending process which forms part of the wall of the neural canal, and a horizontal process terminating distally in the interossicular ligament. In the light of such facts the nature of the intercalarium presents no special difficulty. With the Siluridæ, however, it is otherwise. In all previously investigated species the intercalarium is represented by a variously shaped nodule of bone imbedded in the interossicular ligament, and has no connection with the walls of the neural canal, or with any vertebral centrum. On this point, RAMSAY WRIGHT (44) remarks, "the Siluroids do not afford the necessary material for determining the homology of the incus* on account of its reduced condition" (p. 109). The condition of the ossicle in at least some Characinidæ is essentially similar, and this led SAGEMEHL (33) to regard it as a free metamorphosed rib belonging to the second vertebra. We are able to show, however, that the Siluridæ do afford the necessary evidence for determining the nature of the ossicle. Our discovery of an intercalarium in the Siluroids *Macrones*, *Liocassis*, *Pseudobagrus*, &c., which has an ascending process forming part of the wall of the neural canal, and a horizontal process which terminates distally in a nodule imbedded in the interossicular ligament, at once brings the Siluridæ into conformity with the Cyprinidæ, and establishes the identity of the ossicle in the former family. The correctness of this conclusion is confirmed by the fact that the ascending process of the ossicle in these Siluroids is situated between the paired foramina for the exit of the roots of the second and third spinal nerves from the neural canal. The condition of the ossicle, in the majority of Siluroids, is clearly due to degeneration from its more primitive condition in *Macrones*; and from this point of view such genera as *Callichrous* and *Cryptopterus*, in which the ascending process has vanished, and the horizontal process and its distal expansion alone remain, must be regarded as supplying an intermediate stage between the two extremes. A further question arises as to whether, in addition to a modified neural arch, the intercalarium did not originally include an element comparable to a transverse process. We are inclined to think that it did, and that the horizontal process of the ossicle, when present, represents the modified transverse process of the second vertebra. In its origin from the neural arch or ascending process, the horizontal process conforms precisely to the contiguous transverse processes of the fourth and fifth vertebræ, which spring in exactly the same way from the neural arches, and not from the centra of their respective vertebræ.

V.—THE PHYSIOLOGY OF THE AIR-BLADDER AND WEBERIAN MECHANISM IN THE SILURIDÆ.

A. *Siluridæ normales.*

From the morphology of the air-bladder and Weberian ossicles, we may next proceed to discuss how far the facts elucidated in the preceding sections of this paper throw any light on the vexed question of their physiology.

There is a strong *à priori* probability that the Weberian mechanism is physiologically related to one of the several functions that have been ascribed to the auditory organ or to the air-bladder, but to which of them is a question by no means easy to answer. A preliminary difficulty to be encountered is the complex physiological character of the two organs; and, apart from our imperfect knowledge of the physiology of the several functions assigned to each, and especially in the case of the internal ear of Fishes, a further difficulty is afforded by the total absence of any experimental evidence directly bearing on the functional significance of the Weberian ossicles. And, while we desire to emphasize the danger of making physiological deductions from facts of a purely anatomical nature, no other course has yet been adopted by previous writers on this subject, and, at present, this is the only one open to us; consequently, any conclusions based upon data so frequently misleading and unreliable must partake rather of the nature of suggestions, and be accepted with considerable reserve. With the qualification rendered necessary by these considerations, some light may possibly be thrown on this difficult problem by a careful inquiry as to how far the Weberian ossicles, and the coadapted parts of the air-bladder and internal ear, are anatomically fitted to act as subsidiary or accessory structures in connection with any of the several functions assigned to either the air-bladder or internal ear, while unsuited for association with others. By this means it may at least be possible to eliminate certain functions from any further consideration, and thereby considerably narrow the scope of future inquiry.

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* (= intercalarium.)

With this object in view, we propose in this section of our paper to discuss (1) how far the function of the Weberian mechanism is conditioned by the anatomical structure of the air-bladder and internal ear; (2) to which of the known functions of the air-bladder and auditory organ the Weberian ossicles are to be regarded as accessory structures; and (3) the use and advantage of the Weberian mechanism to the Fish possessing it.

1. In all the Siluridæ normales the air-bladder may be regarded as consisting of two intercommunicating, but physiologically distinct, portions—a posterior, represented by the two lateral compartments, which is indistensible and inelastic, and always of greater internal capacity; and an anterior, which, on the contrary, is always more or less elastic and expansible, but of less internal capacity than the former. The distensibility of the anterior chamber, however, is by no means uniform in all directions; on the contrary, and for reasons already given,* this portion of the bladder is absolutely inexpansible, except laterally at right angles to its antero-posterior axis. From the mode in which the fibres forming the lateral walls of this chamber converge in each half of the dorsal wall and become inserted into the convex outer margin of the crescentic process of the tripus, it becomes still further obvious that it is only by inward or outward bulgings of the lateral walls that variations in the internal condition of the air-bladder are able to set in motion the series of Weberian ossicles. It is scarcely necessary to point out that by this restriction of the expansion or contraction of the anterior chamber to movements of its lateral walls, which alone

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* See pp. 93–95, 98, and 239–241.

are directly connected with the tripodes, the Weberian ossicles are rendered more susceptible, and, therefore, capable of responding to smaller variations of internal gaseous tension, by whatever cause produced, than if the anterior chamber were equally elastic and expansible in all directions. The increased delicacy of the Weberian mechanism in the normal Siluridæ, as compared with other Ostariophyseæ, is probably the cause of the more extensive anchylosis of the anterior vertebræ, and their rigid articulation with the skull. If the anterior vertebræ were flexibly articulated with one another and to the skull, so as to be able to participate in the lateral flexion of the vertebral column in ordinary locomotion, while at the same time these vertebræ and their processes retained their close relation to the dorsal surface of the air-bladder, the anterior chamber and Weberian ossicles could hardly fail to be affected by muscular compression. Consequently, the anchylosis of those vertebræ which are specially related to the anterior chamber becomes almost a necessity in the Siluridæ if the Weberian mechanism is to remain unaffected by the more or less violent shocks produced by variations of muscular contraction and relaxation. The posterior portion of the air-bladder, represented by the two lateral compartments, lies free in the abdominal cavity and is not specially related to any skeletal elements, and anchylosis in this region does not, therefore, take place. From the position and shape of the tripus and its mode of articulation with the centrum of the complex vertebra, as well as from the relations and attachments of its crescentic process to the fibres converging from the corresponding lateral wall of the anterior chamber, it will follow that any inward or outward movement of the lateral wall will necessarily cause the crescentic process to move either inwards or outwards, while the anterior process of the same ossicle will execute similar movements, but in inverse order. In all such movements the tripus constitutes a lever of the first order, the fulcrum of which is represented by the articulation of the articular process of the ossicle with the complex centrum. The relative lengths of the two arms of the lever, that is to say, the anterior and crescentic processes, vary somewhat in different Siluroids, although within limits so narrow that in the great majority of the normal forms that came under our notice the two were of approximately equal length. Very exceptionally the anterior process may be slightly the longer of the two, and, consequently, like the long arm of a lever, gains in amplitude of movement what it thereby loses in force. Any inward or outward movement of the anterior process of the tripus will impart either a push or a pull to the interossicular ligament, and finally to the spatulate process of the scaphium, which, therefore, moves either inwards or outwards by a corresponding rotation of that ossicle on its condylar and ascending processes, and with every such movement of the scaphium a forward or backward impulse will be given to the perilymph of the atrial cavities. The characteristic curvature of the crescentic process of the tripus apparently serves no other purpose than that of increasing the surface required for its connection with the fibres of the air-bladder.

The precise mode in which movements of the anterior process of the tripus are transmitted to the scaphium requires a more critical examination than has yet been given to this point by previous writers. Although of considerable thickness in proportion of its length, the interossicular ligament cannot be regarded as a rigid structure, but rather as being more or less compressible, and hence the immediate result of any slight inward movement of the anterior process of the tripus towards the scaphium, following upon any outward bulging of the corresponding lateral wall of the anterior chamber, will be the compression of the ligament in the direction of the length of its component fibres, and this must necessarily lead to an outward bulging or swelling analogous to that of a contracting muscle, the swelling taking place at right angles to the direction in which the force tending to produce compression is applied. Under such circumstances, no immediate inward movement of the spatulate process of the scaphium takes place. Conversely, any slight outward movement of the tripus that might subsequently take place would at first only have the effect of straightening, as it were, by a pull, the outwardly bulging fibres of the ligament. Hence, it may be concluded that relatively slight incursions or excursions of the anterior process of the tripus will produce no effect on the scaphium, and that only movements of the tripus, of greater amplitude than those now under consideration, are competent to bring about corresponding movements of the scaphium, or affect the fluids of the internal ear. But, apart from the interossicular ligament, there are other reasons for the belief which we certainly entertain, that the Weberian ossicles are but ill-adapted for the transmission of movements caused by the slight inward or outward bulging or vibration of the lateral walls of the anterior chamber. The size of the Weberian ossicles, or at all events, of the tripus; the character of the articulation between the articular process of the tripus and the centrum of the third vertebra, which, in some Siluridæ (*e.g.*, *Auchenipterus nodosus* and *A. obscurus*) is effected by the actual but flexible continuity of that process with the centrum in question; and the fact that all movements of the ossicles, or at least of the tripus, must take place in the loose, fluid-infiltrated connective tissue of the saccus paravertebralis—seem to afford strong additional evidence that the Weberian apparatus is far better adapted to register the more forcible, even if more gradual distensions or contractions of the anterior chamber, rather than slight or rapidly recurring vibrations of its lateral walls. Among other facts tending to the same conclusion may be mentioned the extreme thickness of the walls of the air-bladder in many Siluroids, and in certain genera and species (*Osteogeniosus*, *Ælurichthys*, and several species of *Arius*), this feature is still further emphasized by the development of vertically-disposed, buttress-like, aggregations of the fibres forming the inner stratum of the tunica externa of the lateral walls of the anterior chamber. The peculiarities of the interossicular ligament and the inertia of the Weberian ossicles, taken in conjunction with other anatomical features more directly pertaining to the structure of the air-bladder itself, seems to us to offer an insuperable objection to any theory of the function of those ossicles which relies upon their capacity to be affected by, or to transmit to the internal ear, vibrations or other movements of the lateral walls of the anterior chamber that are of slight amplitude and rapid recurrence from whatever source derived. In fact, it would almost seem as if the interposition of a lax, or rather compressible ligament between any two of a series of three movable ossicles, were a special contrivance for the express purpose of preventing the internal ear from becoming susceptible to any but the comparatively grosser changes that take place in the internal condition of the air-bladder. It is also difficult to avoid the conclusion that the Weberian ossicles constitute a mechanism which, while not sufficiently delicate to be capable of transmitting to the internal ear slight variations in the condition of the gaseous contents of the air-bladder, is, nevertheless, very susceptible to all such changes that exceed a certain minimum.

The function of the intercalarium is not very clear in those Siluridæ in which it is represented by a mere nodule of bone imbedded in the interossicular ligament, unless it is to impart some slight rigidity to that structure, but even if this be the case the ligament still remains sufficiently lax or compressible to warrant the physiological conclusion to which reference has just been made. In the very limited number of instances (*e.g.*, *Macrones*, *Pseudobagrus*, *Liocassis*, etc.) where the intercalarium not only consists of a horizontal process with its distal end imbedded in the interossicular ligament, but in addition, of an ascending process lying in the fibrous wall of the neural canal between the exoccipital and the arch of the third vertebra, it is also difficult to see that the ossicle can have any other function assigned to it than that of slightly stiffening the ligament in question. Some light, however, may be thrown on this point by a comparison of the position and relations of the intercalarium in the two families of the Siluridæ and Cyprinidæ. In the latter family, where the ossicle is represented by a Y-shaped bone having its two arms articulated with the lateral surface of the conjoined second and third vertebræ, and the distal extremity of its outwardly-directed stem inserted into the centre of the interossicular ligament, the scaphium is somewhat more anterior in position than the anterior extremity of the tripus, and consequently the ligament in passing between the two ossicles, assumes a direction which is somewhat oblique from behind forwards and inwards. Not only is the ligament more oblique in direction, but it is of also greater relative length and thinness than in the Siluridæ. In this case there can be but little doubt that the intercalarium functions as a pulley, and by moving through the arc of a small circle coincidently with the motion of the tripus, so alters the direction of the pull of the interossicular ligament as to enable the latter more directly to exert its full force on the scaphium. In the absence of an intercalarium, or if that ossicle were in the same condition as it is in the great majority of the Siluridæ, the length, thinness, and compressibility of the ligament would be such that it is difficult to see how any but the most extensive volumetric variations of the air-bladder could possibly have any effect either on the scaphium or the internal ear. In the Siluridæ, on the contrary, the spatulate process of the scaphium is situated exactly opposite and internal to the anterior extremity of the tripus, and hence the transversely-disposed interossicular ligament passes straight from one ossicle to the other, and no sesamoid or pulley-like action of the intercalarium is necessary. We are, therefore, inclined to regard the intercalarium in the Cyprinidæ as fulfilling its primary function of giving increased leverage to the action of the interossicular ligament, such a function being necessitated by the relative positions of the two ossicles between which this ligament extends ; while in the Siluridæ, on the other hand, from the altered relation and more direct juxtaposition of the scaphium and tripus, the need of an intercalarium is no longer felt; and consequently this ossicle in the vast majority of the normal Siluridæ becomes the comparatively functionless vestige of a physiologically more important structure in the Cyprinidæ. At all events this conclusion seems to receive considerable support from the fact that the difference in the relative positions of the scaphium and tripus seems to be a constant character in all hitherto investigated species of the two families, and correlated with such differences there are also certain almost equally constant modifications in the condition of the intercalarium, to the extent that in nearly all Siluridæ the ossicle has lost all connection with its vertebral centrum, and becomes but a comparatively insignificant nodule in the interossicular ligament, whereas in all the Cyprinoid Fishes, including even those with abnormal air-bladders, the intercalarium retains both its insertion into the ligament as well as its fulcral connection with the centrum of the second vertebra.

The function of the radial fibres of the tripus seems to be that of antagonizing the outward pull which those fibres that pass from the convex side of the same process into the dorsal and lateral walls of the anterior chamber exert upon the tripus during any lateral distension of that part of the air-bladder. When distension subsides the pull of the previously tensely stretched radial fibres causes the crescentic process to move inwards to its normal position of close relation to the lateral surface of the complex centrum. Normally the two sets of fibres exactly counterbalance each other, and according as the volume of the anterior chamber is increased or diminished by lateral expansion or contraction, so will the pull of one set of fibres predominate over that of the other. In one or two instances (*e.g.*, *Auchenipterus*) where the elasticity of the articular process of the tripus functionally replaces the radial fibres, the latter are but feebly developed.

Any push or pull given to the spatulate process of the scaphium by the inward or outward movement of the anterior process of the tripus must also cause the former to move inwards or outwards, and by so doing slightly decrease or increase the size of the atrial cavities. The immediate effect of this will be to cause either a forward or a backward flow of the fluids of the two cavities. The extent to which the atrial cavities will be increased or diminished in size by these means will, of course, primarily depend upon the amount of lateral contraction or distension to which the anterior chamber of the air-bladder is liable, but the result will be that any motion, whether actual or molecular, imparted to the fluid contained in those cavities must be transmitted to the endolymph of the sinus and ductus endolymphaticus, and eventually to that which fills the two sacculi, and finally act as a stimulus to the sensory epithelium of the latter. RAMSAY WRIGHT has briefly discussed the influence exerted by the movements of the scaphia on the fluids of the membranous labyrinth, and with his conclusions we entirely agree. With every inward movement of the spatulate process of the scaphium "the cavity of the atrium sinus imparis is diminished, and the contained fluid urged onward. As the result of more fluid being forced into the cavum sinus imparis the saccus endolymphaticus, which floats freely in it, must be compressed and a current of endolymph urged forwards which must impinge very directly on the macula acustica sacculi of each side. The position of the maculæ with relation to the saccus and ductus endolymphaticus would appear to render unnecessary the special maculæ described by NUSBAUM (29) in *Cyprinus*. In any case the altered tension in the anterior part of the air-bladder will be brought within range of perception by the auditory nerve" (43, p. 383). If any doubt attaches to these statements it is whether the saccus endolymphaticus undergoes actual compression, or that as a consequence an actual flow of endolymph takes place towards the sacculi. It may more probably be the case that movements of the two scaphia produce oscillation waves in the fluids of the atrial cavities and the cavum, and that such waves cause similar disturbances in the endolymph of the saccus and ductus endolymphaticus, but without there being any actual flow towards the sacculi. There can be but little doubt that the sensory epithelium of the two sacculi is solely concerned in the transmission of stimuli received through the Weberian mechanism to the auditory nerve, for the oblique valve in the ductus sacculo-utricularis must prevent the extension of any disturbance in the endolymph of the sacculi to the utriculi, or to the semi-circular canals and their ampullæ.

HASSE'S suggestion (18) that the propulsion of fluid into the atrial cavities and the cavum sinus imparis may, by radiation of pressure, directly stimulate either the spinal cord or the base of the brain, has been successfully opposed by RAMSAY WRIGHT, who expresses his belief "that it is solely through the auditory nerve, and especially through its saccular branches, that the central nervous system is informed of the movements of the 'malleus' and 'stapes,' and consequently the state of distension of the air-bladder" (*loc. cit.*, p. 384).

The peculiar sac (receptaculum dorsale) which in *Amiurus catus* lies on the dorsal side of the medulla oblongata, and ends blindly behind in two lobes but anteriorly communicates with each atrium at the point where the latter becomes continuous with the cavum sinus imparis may, as RAMSAY WRIGHT (*loc. cit.*, p. 384) not unreasonably suggests, act as a reservoir for the fluids of the atrial cavities, or may serve to receive any excess driven out of the atria by the movements of the scaphia, and therefore prevent shocks of undue force from being imparted to the endolymph of the saccus endolymphaticus, and eventually to the nerve endings of the maculæ acusticæ of the sacculi. A similar function may possibly be assigned to the receptaculum dorsale described by us in *Macrones nemurus.*[*]

No differential action of the two sacculi can possibly take place, at all events so far as impulses received through the Weberian mechanism are concerned, since the only channel through which any movement initiated in the fluids of the atrial cavities by the motion of the Weberian ossicles can reach them is the median and unpaired sinus endolymphaticus; hence it must follow that each sacculus will be affected by any such disturbances to an equal extent and at the same moment.

It may be well to emphasize the fact that, whatever may be the force which sets the Weberian ossicles in motion, there are no obvious adaptations for increasing its intensity in the course of transmission to the sensory epithelium of the inner ear, and if, as we believe will prove to be the case, it is the variations in the volume of the gas contained in the air-bladder under the influence of different hydrostatic pressures, which condition the lateral expansion or contraction of the anterior chamber, it is obvious that the force exerted on the Weberian ossicles will be too considerable for there to be any use of increased leverage in order to augment the impulse imparted to the fluids of the internal ear. We shall again refer to this point in discussing WEBER's auditory theory of the function of these ossicles.

On the whole, and apart from any predisposition in favour of any particular theory, the impression left upon our minds by a consideration of the extent to which the physiology of the Weberian mechanism is conditioned by the more obvious features in its structure and relations to the air-bladder is, that it is not adapted for the transmission of the smaller changes of whatever nature that may take place in the condition of the gaseous contents of the air-bladder; still less is the mechanism adapted for the transmission of any rapid vibratory impulses that may be communicated to the contained gases; on the contrary, the mechanism would seem to be admirably fitted to acquaint the Fish with the occurrence of the grosser volumetric variations that from time to time may affect the entire gaseous contents of the air-bladder.

2. The second point for consideration is—to which of the several known functions of the air-bladder and internal ear are the Weberian ossicles to be regarded as accessory structures.

As we have already pointed out, an initial difficulty in the way of any attempt to solve this question is the complex physiological character of the two organs which the Weberian ossicles bring into functional relations. At least two distinct functions must be considered in connection with the auditory organ, (1) audition, and (2) equilibration, or orientation;[†] while the air-bladder in different Fishes is even more complex in function, more so possibly than any other organ. Among the various uses attributed to the air-bladder by different writers may be mentioned (1) phonation; (2) respiration; (3) an accessory to audition; or (4) its function may be purely hydrostatic.

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[*] See p. 81.

[†] As a sequel to the researches of GOLTZ and others among Vertebrata, mention may be made of the fact that DELAGE (11) and ENGELMANN (12) have shown that it is highly probable that the so-called

Certain of these functions can at once be eliminated from any discussion as to the physiological significance of the Weberian ossicles.

Equilibration is one of these. No conceivable changes are likely to take place in the condition of the gaseous contents of the air-bladder as the result of any movement of rotation or oscillation on the part of the Fish, and without such changes of a degree and kind calculated to produce movements of the lateral walls of the anterior chamber, no motion of the Weberian ossicles could take place, neither would any change occur in the endolymph of the semicircular canals, either in the form of intra-labyrinthic pressure, as GOLTZ himself proposed, or by an actual flow, as maintained by MACH, BREUR, and CRUM-BROWN. But even supposing that movements of oscillation or rotation were competent to so alter the internal condition of the air-bladder that increased pressure or a flow would be produced in the fluids of the atrial cavities, and secondarily, in the sinus and ductus endolymphaticus and the two sacculi, the presence of an oblique valve in the ductus sacculi-utricularis would certainly tend to hamper, even if it did not entirely prevent, the extension of such disturbances into the semicircular canals, where the function of equilibration is specially located. And, finally, it may be mentioned that even if no other difficulty existed, the fact that no differential action of the two membranous labyrinths could take place as the result of stimuli received from the air-bladder through the Weberian ossicles, must be fatal to the existence of any functional relations between equilibration and the Weberian mechanism.

In addition to the various other methods by which voluntary sounds are produced in different Fishes, the air-bladder not infrequently shares in the function of phonation. Such sounds are either produced by the vibration of the internal annular diaphragm,* or by the vibration of certain extrinsic muscles,† the air-bladder in the latter case intensifying the sound produced by acting as a resonator. DUFOSSÉ (*loc. cit.*) is also of opinion that some Ostariophyseæ (*e.g.*, some Cyprinidæ and one or two Siluridæ) produce breathing noises ("les bruits de souffle") by the expulsion of gas from the air-bladder through the ductus pneumaticus, and it has been suggested that the grunting sounds emitted by *Clarias*‡ have a similar origin.

The possibility that the Weberian ossicles have anything whatever to do with phonation, either in the Siluridæ, or in other Ostariophyseæ, is very remote and need be but briefly considered.

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auditory organs of many aquatic Invertebrata may perform singly or conjointly the functions of equilibration and audition.

* MOREAU (27A).

† DUFOSSÉ (11B).

‡ Quoted by DAY in "Instincts and Emotions in Fish," 'Linn. Soc. Trans.' (*Zool.*), vol. 15, 1880.

It is by no means obvious that DUFOSSÉ is correct in regarding all these examples of breathing noises as genuine instances of the production of voluntary sounds, still less is it clear that the emission of such sounds is in any way a part of the normal function of the air-bladder. In none of the Siluridæ or Cyprinidæ that DUFOSSÉ mentions is there any mechanism by which the expulsion of gas from the air-bladder through the ductus pneumaticus in sufficient volume or with sufficient rapidity to produce audible sounds could be effected. Any such expulsion of gas seems only to take place under the influence of a diminution in the pressure of the superincumbent water, in which case the expansion of the gas might lead to its forcible escape from the air-bladder and at the same time to the emission of a breathing noise. This certainly does occur in many Physostomi, and may be utilized by the Fish as a means of adjusting the volume of its air-bladder and the specific gravity of its body to varying external pressures, but there is certainly no clear evidence that this method is ever employed in the production of normal *voluntary* sounds in the Ostariophyseæ, and even if it were the case the effect could only be produced at the expense of a considerable disturbance both of the normal equilibrium of the Fish in the water and of its locomotor activity. We are strongly inclined to the opinion that although sounds may indirectly have their origin in the air-bladder, they have no relation to it other than as accidental accompaniments in the exercise of its normal hydrostatic function.* In one example cited above (*Clarias*) it is almost certain that the grunting sound which the Fish is said to make could not be caused by the voluntary expulsion of gas from the air-bladder, inasmuch as this organ is not only rudimentary but almost completely encapsuled by bone. Eliminating such doubtful examples of the association of the air-bladder with phonation in a few Siluridæ and Cyprinidæ, it may be urged with regard to the rest that the comparative rarity of well authenticated instances of the production of voluntary sounds, the absence of extrinsic muscles in all but a few genera (Pimelodinæ), and the want of internal vibratory diaphragms, or other obviously vocal structures, are quite sufficient to prove that the air-bladder takes little or no part in this function, at all events, by any of the ordinary methods known in other Fishes. This conclusion seems to us to apply not only to the two families referred to above, but to all other Ostariophyseæ about which reliable information can be obtained, and to warrant the exclusion of phonation from further consideration in connection with the Weberian mechanism.

With regard to respiration the air-bladder in different Fishes is said to be related to this function in one of two ways, acting either as a lung subsidiary to the gills, or as an oxygen reservoir.

There is no satisfactory evidence that respiration can be effected by the transit of air to and from the air-bladder through the ductus pneumaticus in any Physostomi. Many Fishes frequently resort to the surface and swallow air, which may either act directly on the gills, or on accessory respiratory organs, but the somewhat prevalent impression that some Physostomi are capable of inhaling air through the pneumatic duct rests upon no satisfactory foundation and may be dismissed from consideration.*

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* For these reasons, and in the absence of definite experimental evidence, we cannot at present accept SÖRENSEN'S ingenious theory that the extrinsic muscles of the air-bladder in the Pimelodinæ and the "elastic-spring" apparatus of other Siluridæ are solely subordinate to the voluntary production of sounds.

On the other hand, there is a large body of experimental evidence for the belief that the air-bladder has an important, though secondary, relation to respiration by acting as a reservoir for the superabundance of oxygen which is taken into the blood through the gills, and subsequently re-absorbed from the air-bladder into the blood when the Fish is in water containing but little of that gas in solution.† It seems clear, nevertheless, that, however important this secondary relation of the air-bladder to respiration may be in Fishes in general, there can be no physiological connection between it and the Weberian mechanism. The function of the air-bladder as an oxygen reservoir is, to say the least, as characteristic of those Fishes in which a Weberian mechanism is absent, as it is of those in which it is present. In fact, MOREAU'S researches go much further than this, and prove to the point of actual demonstration that of the Fishes with which he experimented those provided with a Weberian mechanism had relatively but little capacity for absorbing oxygen from the air-bladder, when placed under conditions likely to cause asphyxia, *i.e.*, in water deprived of its oxygen, whereas many other Fishes belonging both to the Physoclist and Physostome divisions of the Teleostei, in which the Weberian apparatus is wanting, had a far greater capacity for absorbing oxygen under similar conditions than the former. MOREAU has also shown that a marked capacity for oxygen absorption is always associated with the presence of retia mirabilia in the walls of the air-bladder, and these structures, as we have already pointed out, are invariably absent in all Siluridæ, and, so far as we are acquainted, in all the remaining Ostariophyseæ.

Dismissing respiration, we may next consider the much more difficult and debatable question whether these structures can be regarded as in any way subsidiary to the function of audition.

Our knowledge of the physiology of hearing is mainly confined to the higher air-breathing Vertebrata, and but comparatively little is experimentally or certainly known at present about this function in Fishes. The conditions of subaqueous audition are in several respects very different from those in air. Not only do sound vibrations in water travel with more than quadruple the rapidity with which they are transmitted in air, but they can be appreciated at far greater distances. There is, in fact, a closer analogy between water and solid bodies than between water and air, so far as the transmission of sound vibrations is concerned. These facts may, to some extent perhaps, be physiologically illustrated by the statement that the relations of the auditory organ of a Fish to a sounding body in water are not very dissimilar to those of an air-breathing Vertebrate when its skull is directly connected with the source of sound. That this is to some extent true is borne out by experiment. In making their celebrated experiments on the transmission of sound in the water of Lake Geneva, COLLADON and STURM* found that sound vibrations, too feeble to produce any appreciable effect on the external surface of the skull when they passed through air could, nevertheless, strongly impress the ear when they were propagated in water and the head of the observer was completely immersed in the fluid. (2.) The same observers also remarked that while the vibrations passed with difficulty from water to air the converse was also true. For Fishes in general, therefore, we are unable to see that there is any need to assume, in the absence of any experimental proof to the contrary, that the essential conditions of subaqueous audition are very different from those in air, except in so far as the physical differences in the conductivities of the respective media are concerned. Sound waves produced by any sounding body in the water and impinging upon the surface of the Fish's skull will readily be transmitted to the internal ear, and such sounds will in all probability be heard with greater rapidity and from greater distances than could possibly be the case under similar conditions in air. In the special case of those Fishes with a Weberian mechanism the question becomes much more complicated, and in dealing with it we shall confine ourselves to the Siluridæ more particularly, although, with slight and unimportant modifications, the same line of argument will be applicable to all other Ostariophyseæ.

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* JOBERT'S experiments (20) to the contrary are, in our own opinion, not conclusive.

† See MILNE-EDWARDS (25), and GOURIET (13A).

WEBER himself not only regarded the ossicles which bear his name as homologous with the incus, malleus, and stapes of the Mammalian ear, but attributed to them an almost exactly similar function. He imagined that sound waves impinging on the surface of the body ultimately affected the air contained within the air-bladder, which organ then acted as a resonator, and by means of the Weberian ossicles transmitted the vibrations to the internal ear. Presumably, the only way in which sound waves can affect the Weberian ossicles and internal ear is by traversing the body wall of the animal and throwing into vibration the air in the air-bladder, which in turn may be conceived as impinging upon the only portions of the bladder at all likely to be capable of vibratory motion, viz., the lateral walls of the anterior chamber; the vibration of these walls might initiate corresponding vibrations in the series of ossicles considered as a rigid whole, and such vibrations through the movements of the scaphia may be supposed to affect the perilymph of the atrial cavities, and eventually the endolymph of the internal ear itself. If WEBER's theory be true the air-bladder must necessarily become an important accessory to audition in all Fishes in which this peculiar mechanism is present. In ordinary Fishes the only sound waves capable of acting as stimuli to the auditory nerves will be those that fall directly on the skull, but in those that possess WEBER's ossicles sound waves impinging on the general surface of the body may, through the air-bladder, become convertible into auditory stimuli.

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* "Mémoire sur la compression des liquides," 'Mém. de l'Académie des Sciences,' vol. 5, p. 346.

From the date of the publication of WEBER's memoir until the appearance of HASSE's paper (18) in 1873, the majority of writers on this subject have more or less explicitly accepted WEBER's views with but little or no qualification, and the term "auditory," as applied to the ossicles, still lingers as an interesting survival of the notion which he entertained of their function. But in addition to those who, like WEBER, apparently regard the Weberian ossicles as related solely to audition, there are others who, while assigning a very different primary function to those structures, are not altogether prepared entirely to exclude the possibility that they may still be, in some subordinate degree, accessory to the function of hearing, and among such writers must be included HASSE—the first opponent of WEBER's theory—and RAMSAY WRIGHT.

Apart from the *a priori* probability that the existence of an anatomical connection between the air-bladder and the internal ear, is to render the former a physiological accessory to audition, and the apparent analogy between the Weberian ossicles and the auditory ossicles of the higher Vertebrata, there is but little to be said in favour of WEBER's view, and even this argument may be used in quite another way and with equal force, for it is at least as likely that the Weberian ossicles are related to some function of the air-bladder as that they are subsidiary to any function of the internal ear. On the other hand, there are many and weighty reasons for the belief that WEBER's theory is absolutely untenable, and of these we may direct attention to the following :—

(1.) The imperfections of the air-bladder and the Weberian mechanism considered as structures accessory to audition. The gravest objections to the theory certainly come under this head. It may be objected—

(*a.*) That sound vibrations pass with great difficulty from water to air, and hence, if such vibrations are to pass at all from the external medium to the gases contained within the air-bladder, the transmission must be accompanied by a considerable loss of intensity, and the effect upon the latter can be but slight. The intervention of a solid medium between the external surface of the body and the fluids of the internal ear, such as may be found in the bones of the skull, would afford a far better channel for sound conduction than a membranous air-containing sac.* Moreover, although this objection does not apply to the Siluridæ with lateral cutaneous areas, the sound waves in passing from the exterior to the gases of the air-bladder must be greatly retarded in most Ostariophyseæ by having to traverse, not only the lateral muscles of the body wall, but also the air and fluid infiltrated spaces or organs of varying densities by which the bladder is surrounded.

(*b.*) Assuming, in spite of this difficulty, that the air in the air-bladder can be thrown into vibration, it may yet be objected that in many Siluridæ the walls of that organ are too thick to admit of their vibrating synchronously with rapidly recurring sound waves. This objection may certainly be emphasized in those instances in which the walls of the air-bladder are specially thickened where alone their vibration can be conceived as likely to produce corresponding movements in the Weberian ossicles, viz., the lateral walls of the anterior chamber. And, moreover, in the case of all the remaining families of Ostariophyseæ, where the anterior chamber is not specially damped in particular regions through contiguity with suitably modified portions of the skeleton, its walls would probably vibrate to an equal extent in all directions, but, as only those vibrations which affect the lateral walls, or take place transversely, are competent to impart their motion to the Weberian ossicles, there must, in such cases, be a considerable loss in the intensity of the final effect produced on the internal ear; and, hence, in dealing with the question of the fitness of the walls of the bladder to be affected by, or to transmit to the Weberian ossicles, delicate wave impulses in the contained gases, we cannot but regard this objection as a serious one.

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* The minute size of the external auditory meatus in some aquatic mammalia (Cetacea) suggests that even in these animals the sound waves, which are effective as auditory stimuli, must traverse the cranial bones.

(c.) It may be further objected that the Weberian ossicles do not satisfy the necessary conditions required in a series of movably articulated ossicles adapted for the transmission of sound vibrations by vibrating as a rigid whole. In the, in some respects, analogous mechanism of the Mammalian tympanum the auditory ossicles directly articulate with one another without being in any way separated by a fibrous ligament of any description, and hence the ossicles are capable of vibrating as a rigid whole, synchronously with the sound vibrations that impinge on the tympanic membrane, and also of communicating such vibrations to the fluids of the inner ear. The Weberian ossicles, on the contrary, are but ill adapted for any such function. As we have previously pointed out, the inertia of the ossicles themselves, the mode of articulation of the tripodes with the centrum of the complex vertebra, which in some cases is affected by the actual continuity of their articular processes with the centrum in question, and more especially the interposition of a lax, or at all events compressible, ligament in the series of ossicles, are insuperable objections to any theory that requires that these structures should vibrate as a rigid whole, by rapidly recurring movements of slight amplitude, synchronously with the sound waves which, *ex hypothesi*, are produced in the gases of the air-bladder.*

There are also other features in which the Weberian and true auditory ossicles may be compared and contrasted. With auditory ossicles there are almost always certain anatomical adaptations by means of which the effect produced at one end of the series by the direct impact of sound waves is considerably intensified at the other, where the ossicles are in direct relation with the fluids of the internal ear. This effect is usually brought about by the existence of marked disparity in the superficial areas of the tympanic membrane and the membrane of the fenestra ovalis, and, in addition in Mammalia, by the leverage of the ossicles themselves. In one respect the Weberian mechanism may be said to resemble auditory ossicles. The superficial areas of the lateral halves of the anterior chamber of the air-bladder in the Siluridæ vastly exceed the areas of the external atrial apertures, and of the spatulate processes of the Scaphia which close them, and therefore, whatever may be the mode of motion or vibration of the former, the intensity of the final effect upon the latter must be increased in direct proportion to the difference between their respective superficial areas. Nevertheless, it is doubtful if any physiological significance can be attached to this resemblance which, after all, is merely superficial, and, as we have already suggested, is apparently conditioned by the necessarily large relative size of the air-bladder. On the other hand, the leverage of the Weberian ossicles in the Siluridæ is very different from that of the Mammalian auditory ossicles. The approximate equality in the length of the two arms of the lever in the former case is sufficient to prove that no increased effect is gained in the transmission of any form of motion from the walls of the air-bladder to the auditory organ. In fact, so far from there being any special adaptations in the Weberian mechanism for this purpose, which would certainly seem to be necessary in the case of sound transmission, the facts of structure point quite in the opposite direction. The nature of the ligamentous connection between the different ossicles, and the fact that the movements of the Scaphia must take place in a plane at right angles to the posterior entrance of the cavum sinus imparis,* and the division of the neck of the sinus endolymphaticus into the right and left halves of the ductus endolymphaticus at right angles to the former, seem better adapted to diminish rather than intensify the effect produced on the auditory organ by *slight* vibrations or other movements of the walls of the air-bladder.

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* See also pp. 264, 265

(*d*.) HASSE (18), in opposing the application of WEBER's theory to the Cyprinidæ, lays some stress on the objection that the perilymph of the atrial cavities and cavum sinus imparis is contained within the interspaces of a reticular connective tissue, and therefore is ill adapted to transmit vibrations to the endolymph of the sinus endolymphaticus. This objection has considerable force when applied to the Cyprinidæ, and possibly also to many other Ostariophyseæ, but is of little moment so far as the Siluridæ are concerned. On this point we quite agree with RAMSAY WRIGHT's remarks on the Siluroid *Amiurus catus*, which are in complete agreement with our own observations on *Macrones nemurus*. He says, "but in *Amiurus* the fluid in the atrium and cavum is not imbedded in the meshes of the reticular tissue, the wall of the saccus endolymphaticus is so thin that any motion in the surrounding fluid must disturb its contents, and the currents so produced must certainly affect the neuro-epithelium as much, if not far more than the currents produced by sound waves" (43, p. 385). Although this statement to some extent mitigates the force of HASSE's objection in the case of one particular family, yet in all other cases the objection is a forcible one, and the exceptional condition of the Siluridæ in no way lessens the strength of the arguments against WEBER's theory which we have previously urged, and cannot but regard as fatal to it.

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* HASSE (18) directs attention to this point.

(*e.*) Even if the admission be made that the air-bladder and its ossicles are accessory to hearing, the Fish could have no power of appreciating the direction of sounds conveyed to the internal ear by such means. Any cognizance of the varying directions from which sounds may come is generally believed to be due in all vertebrated animals to the differential action of the two ears, but we have already shown* that no such action can possibly take place in response to impulses received through the Weberian mechanism in accordance with WEBER's theory. It would, therefore, seem that any increased acuteness of hearing that might be conferred on the Fish by the air-bladder in its presumptive function as an accessory to audition, would be counterbalanced by the fact that such increase of auditory capacity could not be associated with a corresponding increase in the power of appreciating the direction of sounds. Whatever may be the physiological importance of the sense of hearing in Fishes, whether associated with the pursuit of prey, or as an aid in escaping from enemies, or, as in the case of gregarious Fishes, as a means of keeping together in shoals for breeding or other purposes, the power of appreciating the direction of sounds must be of primary importance in any modification of the auditory organ in the direction of giving to its possessor exceptional powers of hearing.

(2.) Contrary to what might fairly be expected if so complicated a structure as the Weberian mechanism is an accessory to hearing, there is absolutely no evidence of the existence of exceptional powers of hearing either in the Siluridæ or any other Ostariophyseæ.

(3.) Finally, it may be affirmed that there is an alternative view of the function of the Weberian ossicles, which is in perfect harmony with the facts of structure, and is open to none of the objections which can be reasonably urged against WEBER's theory, and also, at the same time, has an important bearing on the locomotor activities of the Fishes concerned.

With the reservation which the entire absence of direct experimental evidence renders absolutely necessary, it may be affirmed that the arguments set forth in the preceding paragraphs are distinctly adverse to the theory that the Weberian ossicles are in any way related to the function of audition, even to the subordinate and qualified extent tacitly suggested by HASSE and RAMSAY WRIGHT; and the solution of this difficult problem must be looked for in some other direction.

Dismissing sound production, equilibration or orientation, respiration and audition from all physiological connection with the Weberian ossicles, we may now consider the sole remaining alternative view—that the ossicles are accessory to the hydrostatic function of the air-bladder. But before dealing with this aspect of the problem it will be advisable to state what is actually and experimentally known as to the hydrostatic function of the air-bladder in Fishes in general.

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* See p. 268.

One of the earliest theories of the hydrostatic function of the air-bladder with which we are acquainted is that propounded by BORELLI in 1685. According to his theory the function of the air-bladder, in its mean condition, is to render the specific gravity of the Fish equal to that of the water in which it lives, and also aid the Fish in its movements of ascent and descent in the water, such movements being due either to an increase in the specific gravity of the animal as the result of muscular compression of the air-bladder, or to the diminished specific gravity which would result from muscular relaxation and the consequent expansion of the contained gases.* From the time of BORELLI until the publication of the results of MOREAU's experimental researches in 1876, the function of the air-bladder proved a fruitful source of discussion among zoologists and comparative physiologists, among whom the names of DELAROCHE, CUVIER, STANNIUS, GOURIET, OWEN, BIOT, MONNOYER, and JOHANNES MÜLLER may be mentioned. Most of these writers, however, adopted the theory of BORELLI with scarcely any modification, and with a like absence of any attempt at experimental proof.

JOHANNES MÜLLER (28), while accepting BORELLI's views for Fishes in general, is responsible for another theory as to the hydrostatic function of the air-bladder in certain Fishes, which has been widely quoted with tacit approval, but like BORELLI's theory, has never received the sanction of experimental proof. MÜLLER's theory is: that those Fishes (Cyprinidæ and Characinidæ) in which the air-bladder is partially constricted into an anterior and a posterior sac, possess the power by muscular contraction of driving the air from one chamber to the other, and thus producing a displacement of the centre of gravity with reference to the longitudinal axis of the animal. By this means such Fishes were supposed by MÜLLER to be able by see-saw movements to vary in a vertical direction the long axis of the body, the fins then causing the Fish to advance in the new direction which the axis of its body had taken.†

More recently the theories of BORELLI and JOHANNES MÜLLER have been successfully opposed on experimental grounds, first, by MOREAU (27), in 1876, and, secondly, by CHARBONNEL-SALLE (6), in 1887. Summarizing the conclusions which these researches appear to justify, it may be affirmed for Fishes in general:—

(1.) That the function of the air-bladder is to render the Fish, bulk for bulk, of the same weight as the medium in which it lives.‡ In this mean condition, or plane of least effort, the Fishes acquire a capacity for the maximum amount of locomotion with a minimum of muscular effort.*

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* It is worthy of notice that the theory usually associated with the name of BORELLI is practically identical with one propounded by the authors of two papers in the 'Phil. Trans.' for 1675, and therefore published several years earlier than the former. See "Conjecture concerning the Bladders of Air found in certain Fishes," and illustrated by an experiment suggested by the Hon. ROBERT BOYLE; and also "On the Swimming Bladders in Fishes," by Mr. RAY (*loc. cit.*).

† MONNOYER (26) on purely theoretical grounds also adopted MÜLLER's theory, but admits his inability to support his conclusions by any experimental evidence.

‡ The experiments of DELAROCHE (11A) prove that a Fish without an air-bladder has a density always

(2.) In its movements of ascent and descent the Fish becomes exposed to augmented or diminished pressure, which in each case varies in amount according to the variable height of the superimposed column of water, and this leads to an expansion or contraction of the air in the air-bladder, and consequently to an increase or diminution in the volume of the Fish itself, and thereby to a corresponding alteration in its specific gravity, which may temporarily remove the animal from its normal plane of least effort.

(3.) The Fish has no power of varying the capacity of its air-bladder by direct muscular contraction, and its re-adjustment to a new plane of least effort results from a gradual increase or decrease in the amount and volume of the contained air to an extent proportional to the new pressure, and due to a corresponding modification of the processes concerned in the secretion or absorption of gas into or from the air-bladder. Hence, by this apparently automatic method of adjustment the Fish will find, sooner or later, and whatever the depth of the water and the amount of external hydrostatic and atmospheric pressure, a plane of least effort where it will again possess exactly the density of the water.

(4.) That JOHANNES MÜLLER's theory of the displacement of the centre of gravity upon a longitudinal axis in the case of Fishes with a two-chambered air-bladder has no foundation in fact.

The conclusions embodied in the preceding sections relate more particularly to the Physoclisti—by far the largest group of Teleostean Fishes—but it may be pointed out that in a general way they apply also to the Physostomi with, however, the qualification that in the great majority of the latter group the mechanical liberation of gas through the ductus pneumaticus takes the place of absorption as a means of adjustment to reduced pressures.

Although an air-bladder is unquestionably an advantage to the generality of Teleostean Fishes, there can be no doubt that its presence is also attended by certain disadvantages which to a greater or less extent limit and control the locomotor activities of its possessor, and that of these the most important is the restriction of freedom of locomotion in the vertical direction, and the consequent limitation of ordinary locomotion within more or less well defined limits above or below a tolerably constant mean position. As MOREAU says, when a Fish is in a plane of least effort the possession of an air-bladder is a distinct advantage, but for rapid changes of level, as in movements of ascent or descent, the air-bladder may prove a considerable disadvantage or even a source of danger. In a Fish, he remarks, which is exposed to artificially diminished pressure the air contained in the air-bladder will

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greater than that of the water, and consequently is never in equilibrium, but must constantly use its fins to prevent itself from sinking.

* A Fish in equipoise in the water resembles the philosophical toy known as the "Carthusian Diver," and the slightest exertion of its fins will readily cause motion in the vertical direction.

tend to assume and retain an augmented volume, and so lessen the specific gravity of the animal that it rises to the surface and can only rest with part of its body in the air. A Fish, MOREAU adds, incurs more danger by rising above its plane of equilibrium than by sinking below this plane for the same vertical distance. On this point reference may be made to SEMPER's remarks (34, p. 340) on the behaviour of the "Kilch" (*Coregonus hiemalis*) when caught in nets and drawn to the surface.* A further proof of MOREAU's conclusions is also afforded by the appearance of certain Fishes when forcibly drawn up or carried to the surface from great depths, or even when trawled from quite moderate depths, both the air-bladder and body being greatly distended, the former not unfrequently ruptured, while there is often a prolapsus from the mouth or anus of the contiguous portions of the alimentary canal. It is perhaps not unreasonable to suppose that a Fish, while under normal conditions and free in the water, is liable to accidents similar in kind if less in degree to those caused artificially by experiment whenever it ventured upon rapid vertical movements in the direction of ascent, accompanied by a marked reduction of pressure. The restriction of the vertical range of the Fish is clearly due to the slowness with which the necessary secretion or absorption of gas takes place, and the facts above quoted are in complete agreement with MOREAU'S experiments, from which it would appear that the adjustment of the volume of gas in the air-bladder to varying pressures is a comparatively slow process, the length of which, however, varies greatly in different Fishes, and under different conditions in the same Fish. In vertical movements, whether slow or rapid, as long as they are confined within certain limits, the action of the fins may prove a sufficient safeguard against the evil results of a too great or a too low specific gravity, but in more extensive movements, more particularly of ascent, the controlling action of the fins may be utterly inadequate to prevent the Fish incurring considerable danger in the way suggested above. Hence, it may be concluded that in the generality of Teleostean Fishes, and more particularly in the Physoclisti, the possession of an air-bladder tends to greatly restrict freedom of locomotion in the vertical direction.

From the conclusions established by MOREAU and CHARBONNEL-SALLE, it becomes obvious that the varying degrees of tension of the gaseous contents of the air-bladder due to variations in the height of the superincumbent column of water, constitute an important factor in the physiology of locomotion in Fishes, and hence, in the absence of any other tenable hypothesis as to its function, there is a strong *a priori* probability that the object of the Weberian mechanism is to acquaint the Fish with the varying degrees of tension to which the air-bladder may be subjected. HASSE (18), who was the first to oppose the then prevalent idea of the air-bladder and Weberian ossicles in the Ostariophyseæ being accessory to audition, without, however, entirely excluding the possibility that such might be the case in some subordinate degree, was also the first to suggest that the object of the mechanism was to acquaint the Fish with the varying tensions of the gases contained in the air-bladder. It is clear, however, that the Fish is not only exposed to varying hydrostatic pressures according to the depth at which it lives, but, at the same time also, to similar variations of atmospheric pressure. According to HASSE's view it is the perception of hydrostatic pressure variations with which the Weberian mechanism is more directly concerned. The late Dr. SAGEMEHL (33) also adopted HASSE's theory, at least so far as to regard the Weberian apparatus as constituting a register of pressure variations, but with this important modification, that it is not hydrostatic but atmospheric pressure which the Fish is thereby enabled to appreciate. Postponing for the present any further reference to HASSE's theory, it becomes necessary to ascertain what measure of truth there may be in SAGEMEHL's barometrical theory, more especially as it has not hitherto been the subject of any critical examination.

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* See also on the same subject R. OWEN (30, p. 496).

Apart from certain anatomical features in the structure of the air-bladder in the Siluridæ on which he lays considerable stress, but which are equally reconcilable with HASSE's views, the only special reason advanced by SAGEMEHL in support of his barometrical theory is that most of the Ostariophyseæ, and especially the Siluridæ, live at the bottom of the water, and hence an air-bladder as a hydrostatic organ is of very little value to them. We must confess that we fail to see that the arguments with which he supports his ingenious theory are conclusive or even weighty, and in opposition it may be urged: —

(1.) That the majority of the Ostariophyseæ are certainly not "bottom" or "ground" Fishes in the same sense as, for example, are the Pleuronectidæ, and unless they habitually rest on the bottom when not in motion by the exercise of their fins like the Flat Fishes, it is clear that an air-bladder as a hydrostatic organ must be as useful to them as to other Fishes. Moreover, there are many facts which tend to prove that whenever any Ostariophyseæ assume a strictly "ground" habit, as, for example, in the Loaches (*Nemachilus*, *Cobitis*, *Botia*, &c.) among the Cyprinidæ, and such forms as *Glyptosternum*, *Exostoma*, *Euclyptosternum*, *Amblyceps*, &c., in the Siluridæ, the air-bladder necessarily becomes useless for hydrostatic purposes, and invariably undergoes more or less degeneration, just as it does in many other Teleostei (*e.g.*, Pleuronectidæ) under similar conditions, whereas by far the great majority of both families possess well developed and normally constructed bladders.

(2.) To a Fish at a depth of, say only 6 feet below the surface of the water, a variation of atmospheric pressure sufficient to raise or depress a column of mercury in a barometer to the extent of half-an-inch will only involve a variation of pressure amounting to less than one-tenth of the already existing hydrostatic pressure, and even this trifling difference will become relatively smaller as the depth at which the Fish lives becomes greater, while the ascent or descent of the Fish in the water to the extent of only 7 inches would certainly mask any variation of atmospheric pressure to the extent indicated. A barometrical variation of even half-an-inch takes place but slowly, and consequently could only be appreciated as distinct from hydrostatic pressure on the somewhat improbable supposition that the Fish remained at exactly the same depth during the whole time that the barometrical variation was in progress. The maximum range of variation in atmospheric pressure, as measured by the barometer, is about 2 inches, but such variations occur only at considerable intervals of time, and then may take many hours to accomplish. But even in this extreme case the atmospheric pressure variation might be negatived as far as the Fish was concerned by ascent or descent in the water to the extent of 27 inches, or more or less completely masked by similar movements of less extent during ordinary locomotion, or by the rise and fall of the tide in the case of a few marine or estuarine Siluridæ.

We have not been able to examine any records relating to barometrical variations in regions where the Siluridæ or Characinidæ are most abundant, but the extent to which the Ostariophyseæ of the British Isles are exposed to atmospheric pressure variations may be readily tested. The only Ostariophyseæ inhabiting Great Britain are the Cyprinidæ, the various species of which are among the commonest and most abundant of British Fishes of fresh-water habitat. Ten genera and fifteen species of Cyprinidæ are known to inhabit this country (10A), and, omitting certain genera* which have small bone-encapsuled air-bladders, there will still remain eight genera and thirteen species with normal, well-developed air-bladders in connection with a Weberian apparatus. It may, therefore, be worth while to ascertain the extent and variety of the barometrical changes to which these Fishes are liable. With this object we carefully examined the variations of the barometer as registered by the barograph of the Birmingham and Midland Institute Observatory during the three years 1886–1888. These records demonstrate (1) that variations of ·50 inch and upwards very rarely occur in less time than 10 hours, and generally require from 12 to 24 hours for their completion. In the three years on only two occasions did a variation so great as ·50 inch occur in less time than 10 hours; (2) variations amounting to ·50 inch and upwards in 24 hours are not common, occurring only fifteen times in 1886, fourteen in 1887, and seven times in 1888; (3) in only one instance did a barometrical rise or fall exceed 1 inch in 24 hours; excluding this very exceptional case, the most striking variations within this period ranged from ·60 inch to ·82 inch, and required from 15 to 24 hours for their completion; such variations happened but seldom, and are recorded only nine times in 1886, four in 1887, and four in 1888; (4) rapid and sudden variations, that is, those occurring within, say, 2–5 hours, are somewhat rare, and, almost invariably, are very small in amount, rarely exceeding ·2 inch. It may be reasonably concluded, therefore, that, so far as the Cyprinidæ of the British Isles are concerned, the variations of atmospheric pressure to which they are liable are too small in amount, too gradual in their progress, and too infrequent to exert any appreciable influence upon an air-bladder already subjected to considerable hydrostatic pressure, especially as the latter, instead of being a constant factor, varies incessantly with almost every locomotor movement of these usually active Fishes, while the Fish can have no power of differentiating the effects due to the incidence of the two pressures. It also seems reasonable so far to extend this conclusion as to infer that if the extent and variety of the barometrical variations above recorded may be regarded as fairly typical of temperate or North temperate regions, the application of Sagemehl's theory to the large number of species of Cyprinidæ which inhabit these areas must be open to very grave objections; and it is at least not improbable that a substantially similar line of argument may be applied with equal force in the case of the remaining Ostariophyseæ which are of tropical or subtropical habitat.

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* *Cobitis* and *Nemachilus*.

(3.) There is no clear evidence that the Ostariophyseæ are in any way different from other Fishes in being specially susceptible to atmospheric pressure variations, or that they possess any special capacity for anticipating impending changes in the weather. The only instance that we have been able to discover has reference to the European "Sheat Fish" (*Silurus glanis*), which is said to become greatly disturbed during the progress of thunderstorms (28A). But this isolated case certainly does not warrant the assumption that the air-bladder and Weberian mechanism are at all concerned in conveying the necessary stimulus to the nervous system of the Fish, inasmuch as at least two alternatives present themselves:—(1) One suggested by Murray, namely, that the Fish is excited by electricity. This is extremely improbable, and is rendered more so when we recall the fact that electrical currents do not readily pass from the atmosphere into water—especially fresh water. (2) The more probable alternative is that thunder, as is well known, causes considerable earth tremblings, which may be easily conceived as a possible source of uneasiness to the Fish.

(4.) Even if the truth of Sagemehl's theory be admitted, it still remains very difficult to imagine what advantage these Fishes could derive from their ability to appreciate variations in the pressure of the atmosphere and consequent impending changes in the weather, nor is it easy to conceive in what way the Fish can adjust its habits or its locomotor activities in accordance with varying meteorological conditions. It might possibly be advantageous for certain marine species of active habit to be able to anticipate a storm and retreat to deeper and calmer waters; but even this advantage could only apply to very few of the Fishes in which a Weberian mechanism is present, and would be altogether superfluous in the case of the fresh-water species which form by far the great majority of the four or five families concerned.

If we regard Sagemehl's barometrical theory as untenable, there remains only Hasse's view that the Weberian mechanism constitutes a register of varying hydrostatic pressures, and this, in our opinion, is the only conclusion that has any foundation in fact. Seeing that the primary and almost universal function of the air-bladder, in spite of the occasional and secondary functions that may, in a relatively small number of Fishes, be grafted upon it, is that of acting as a hydrostatic organ, there is a strong antecedent probability that the Weberian ossicles are directly related to this function. The general structure of the air-bladder, the mode of interconnection of the different Weberian ossicles, and their relations both to the air-bladder and to the internal ear, as well as the relations *inter se* of the different parts of the two last-mentioned structures, are perfectly consistent with this theory, against which no anatomical objections can be urged, and are equally inconsistent with any other at present suggested.

The division of the air-bladder into a small, elastic, and expansible anterior portion, and a relatively large, inelastic, and inexpansible posterior division, renders that organ admirably adapted for the measurement of the varying volumes of the contained gases, inasmuch as the volumetric variations in the relatively large volume of gas contained in the whole bladder will find their expression almost exclusively in corresponding alterations in the size of the anterior chamber through the expansion or contraction of its lateral walls, which alone are directly connected with the recording Weberian ossicles. Regarded, in fact, as an article of physical apparatus, the air-bladder may be compared with such instruments as, for example, the thermometer, by which the expansion or contraction of mercury or alcohol under the influence of changes of temperature is accurately measured. In both instruments there is a relatively large reservoir in free communication with a much smaller one, and the expansion or contraction of the relatively large mass of gas, or fluid, as the case may be, in the larger chamber is measured by the more readily observed expansion or contraction of the contents of the smaller chamber; and hence, there is a close functional parallelism between the anterior and posterior divisions of the air-bladder and the capillary tube and bulb of a thermometer respectively. Similarly it may also be said that the anterior chamber of the air-bladder is, to some extent, constructed on the principle of an aneroid barometer, inasmuch as the susceptibility of the recording lever (Weberian ossicles), connected with the former to the varying volumes of the contained gases, is considerably increased by the comparative rigidity of its anterior, posterior, dorsal, and ventral walls and the consequent restriction of any expansion or contraction to movements of its lateral walls alone, in much the same way that the expansion or contraction of the air contained within the metallic box of the aneroid will find its sole expression in corresponding movements of the flexible upper wall of the box, which alone is capable of transmitting such internal volumetric changes to the external recording lever; in fact, in a certain sense it may be said that the air-bladder of the Ostariophyseæ combines the structural principles of both the thermometer and the aneroid barometer. The varying relative dimensions of the anterior and posterior chambers of the air-bladder in different Siluridæ very probably bear some relation to corresponding variations in the delicacy of the Weberian mechanism as a pressure register in various species, for, as is the case with the analogous parts of the thermometer, the susceptibility of the mechanism should, within certain limits, increase as the posterior chambers become larger and the anterior chamber smaller.

The conclusion to which these facts seem irresistibly to point is still further strengthened by the condition of the air-bladder and Weberian mechanism in the Siluridæ abnormales, but as we shall subsequently have occasion to refer to these Siluroids at some length, we need now only say that in a large number of cases the degenerate and rudimentary condition of these structures is associated with the purely "ground" habit of these Fishes. It is well known that the assumption of a ground habit is in many Fishes accompanied by the degeneration, or even total disappearance, of the air-bladder, which, under such conditions, becomes useless as a hydrostatic organ, even if its retention is not distinctly harmful to the species, and hence its liability to degenerate to the condition of a more or less rudimentary structure, or become completely suppressed. The correlation of a similar habit of life with degeneration of the air-bladder and Weberian mechanism in the particular case of the Siluridæ abnormales, seems to us to furnish almost conclusive evidence that both organs are solely related to the normal hydrostatic function. As an accessory to audition, or even as a register of varying atmospheric pressures, or, indeed, as fulfilling any purpose other than the hydrostatic function, the air-bladder and Weberian mechanism might still be of some utility to these Fishes in spite of their change of habit, and therefore need not degenerate, but the fact that these structures do degenerate under such conditions seems to us to be only reconcilable with the conclusion at which on other grounds we have arrived.

Considered solely from an anatomical standpoint, and with the qualification which the absence of direct experimental evidence imperatively demands, it may be affirmed that Hasse's theory is correct, and that the Weberian mechanism is a pressure register serving to acquaint the Fish with the varying tensions or volumes of the gases contained within its air-bladder, the result of corresponding variations of the hydrostatic pressure. As it is inconceivable that such pressure variations can arise from any other cause than the ascent or descent of the Fish in the water in the course of the ordinary locomotor movements, it may be further concluded that the Weberian mechanism is related to some form of pressure adjustment.

3. If the conclusion at which we have arrived be admissible, the further question—What advantage does the Fish derive from the possession of a pressure register by which it becomes acquainted with the varying degrees of hydrostatic pressure to which it is exposed? or, In what way does the animal respond to the sensory impulses communicated to its central nervous system by the Weberian mechanism and the co-adapted parts of the internal ear? is one to which it is very difficult to return a satisfactory answer. That the Weberian mechanism is of great functional importance to the Fish possessing it admits of no doubt. It is extremely improbable that so complicated and highly specialized a mechanism would have been evolved did it not confer some exceptional advantage upon its possessors, and that this is the case seems to be clearly demonstrated by the significant fact that the presence of a Weberian mechanism is characteristic of nearly all the dominant families of freshwater Teleostei.

Some light may possibly be thrown on this difficult question by a closer comparison of what is experimentally known of the methods of pressure adjustment in Fishes in general, and in the Ostariophyseæ, than has hitherto been made; and if no satisfactory conclusion can be arrived at in this way, some clue at least may be gained as to the direction in which the solution of the problem must be sought for in the future.

Gaseous secretion and absorption are, as we have seen, highly important factors in the majority of Fishes in the adjustment of the volume of gas in the air-bladder to varying hydrostatic pressures, and the conditions under which these pressures take place, have been experimentally investigated by MOREAU. Of the conditions which determine an increase in the rate of secretion of gas into the air-bladder, the most important are (1) repeated abstraction of gas; (2) increase of external pressure;* (3) section of sympathetic nerve; and (4) the presence in the walls of the bladder of special retia mirabilia, or "vaso-ganglia." The process of absorption, on the other hand, is not so well understood, but certain conditions undoubtedly favour its action; these are (1) diminution of pressure, and (2) the existence of retia mirabilia. It will be obvious that the *rapidity* with which the amount of gas in an air-bladder can be augmented or diminished by secretion or absorption, is an important feature in this discussion, for on this will depend the capacity of the Fish to adjust itself to the varying pressures of different levels in ordinary locomotion; but unfortunately MOREAU's experiments do not throw much light on the precise rate at which these processes take place. In many of his experiments, as, for example, in those dealing with secretion, the amount of gas previously abstracted was often so great that the time occupied by the process of secretion to restore equilibrium varied in different Fishes from several hours to several days, and similarly with absorption. No attempt has yet been made to obtain accurate measurements of the precise rate of secretion and absorption, under conditions involving relatively small and gradual variations of level and pressure. Three important facts appear however to be well established: (1) that gaseous secretion and absorption are relatively slow processes in all Fishes; (2) that although retia mirabilia are not indispensable to these processes, there can be no doubt that both take place much more rapidly in Fishes that possess such structures than in those in which they are wanting; and (3) that increased hydrostatic pressure accelerates the rate of secretion, while diminished pressure exerts a similar influence on absorption. With such data as these and other facts supply, we may consider more closely the methods by which in different Fishes the process of pressure adjustment is effected.

In the case of the Physoclisti, which very generally possess retia mirabilia, but no ductus pneumaticus, gaseous secretion and absorption must be the only means of adjustment to varying hydrostatic pressures, but how far this method is available during the changes of level which are encountered in ordinary locomotion is very doubtful, and on this point two suggestions may be made :—(1) It may be possible that the increase of external pressure which accompanies descent, conditions an increased rate of secretion, while a diminution of pressure during ascent involves a like acceleration of the absorptive process, with the result that if such vertical movements are not too rapid or sudden, or too extensive, the processes of secretion or absorption may keep pace with them, and the Fish retain a plane of equilibrium at all levels; (2) without entirely denying that the former suggestion may be true in some subordinate degree, it may yet be conjectured that pressure adjustment by such means is more likely to be of advantage to the Fish during slow or gradual changes of depth, such as may occur in the course of diurnal, seasonal, or other periodic migrations, than in such ordinary and rapid changes of level as are characteristic of normal locomotion. The slow rate of gaseous secretion and absorption renders it difficult to accept unreservedly the first alternative, and this objection is further supported by many features in their habits, which tend to prove that most Physoclisti have but a comparatively restricted vertical range, in so far as ordinary locomotor movements are concerned, as well as by certain facts already quoted.* The second suggestion has also this much in its favour—that even a slow rate of secretion and absorption would be distinctly advantageous to these Fishes in view of the varying pressures to which they are exposed during periods of migration, whether the latter are due to variations in temperature and food supply, or to their breeding habits. On the whole we incline to the opinion that most Physoclists have but a restricted capacity for pressure adjustment during ordinary locomotion, and, in this respect, are less favourably situated than the Physostomi.

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* The effect of pressure on the secretion of oxygen is well illustrated by the observations of BIOT (2), who found that the amount of this gas in the air-bladder increases in direct proportion to the depth at which the Fish is found, and may even amount to 87 per cent.

Leaving the Physoclists, we may next proceed to discuss in the light of MOREAU'S researches the mode in which pressure adjustment is effected in the Physostomi. The great majority of the wholly or partially freshwater families of this group possess both an air-bladder and an open ductus pneumaticus, and to these there is added, in the five families of Ostariophyseæ, a Weberian mechanism. The relatively few Physostomi that possess an air-bladder but have no pneumatic duct, are in precisely the same position as the majority of the Physoclisti, and whatever capacity for pressure adjustment they may possess must be due solely to gaseous secretion and absorption. Of the remainder it will be convenient to consider, in the first place, the Ostariophyseæ, and, secondly, those forms in which the air-bladder is said to possess an open ductus pneumaticus, but has no Weberian apparatus.

From the universal absence of retia mirabilia in all hitherto investigated Ostariophyseæ, it may be legitimately inferred that whatever capacity for gaseous secretion and absorption they may possess must be exercised with extreme slowness, and therefore as a means of pressure adjustment is of minor importance. On the other hand, MOREAU's researches clearly demonstrate that those Ostariophyseæ with which he experimented, possessed the compensating advantage of being able to substitute for absorption the mechanical liberation of gas through the ductus pneumaticus. This conclusion is also supported by many observations which go to prove that while free in the water and under normal conditions, many Cyprinidæ eject gas through the mouth on rising to the surface. Hence it follows that such Physostomi possess a distinct advantage over all Physoclisti in the fact that they can, during ascent, more rapidly adjust the volume of gas in the air-bladder to the requirements of a diminishing pressure by liberating the necessary quantity of gas than by relying solely on the slow process of absorption, and consequently will retain perfect freedom of movement at all points in the course of an upward career, even at the most superficial level. But while it must be admitted that in movements of ascent the Ostariophyseæ possess a distinct advantage over all Physoclisti, it is equally clear that in descent the converse must be true, inasmuch as the absence of retia mirabilia in the former group will render the process of adjustment to an augmented pressure a much slower one than is probably the case in the latter. On the other hand, as MOREAU points out, a Fish will incur more danger by rising above the plane of least effort than by sinking below it for the same distance. It is conceivable that a Physoclist in the course of rapid ascent might so far depart from its normal plane of equilibrium as to be forcibly carried to the surface of the water, and in that helpless condition fall an easy and conspicuous prey to predaceous birds or fishes before it could re-adjust by absorption the volume of gas in its air-bladder to the necessities of a more superficial level. A similar movement of descent, even if increased pressure so reduced the volume of gas in the bladder, and to an equivalent extent increased the specific gravity of the body, as to remove the Fish from its normal equilibrium, would probably involve no special inconvenience, while the gradual secretion of the necessary gas would, sooner or later, restore it to a plane of least effort at the deeper level. Like the Physoclist, and for the same reason, it is probable that the Ostariophyseæ incur no serious disadvantage in descent, although in this group the necessary readjustment by gaseous secretion takes place still more slowly. And, moreover, this apparent disadvantage may be open to some qualification, for it has been experimentally shown that an increase in the rate of gaseous secretion may be brought about not only by augmented pressure, but also by any abstraction of gas that may have occurred during a previous ascent. It is, therefore, possible that such conditions may lead to a more speedy readjustment to the greater pressure of a deeper level than at first sight might be supposed. These considerations seem to us to justify the conclusion that, as compared with the Physoclisti, the Ostariophyseæ possess a greater capacity for adapting themselves to rapid and considerable changes of level, more particularly in the direction of ascent, and that this is the case is to a large extent borne out by what is actually known of their habits and their greater freedom of movement at widely different levels.

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* See p. 278.

The physiological relations of the Weberian mechanism to the hydrostatic function of the air-bladder constitute an extremely difficult problem, and one that can only be satisfactorily settled by experimental inquiry. If retia mirabilia were present, it might be conjectured that the Weberian ossicles formed part of a reflex mechanism by which the varying tensions of the gases in the air-bladder were rendered capable of so affecting the central nervous system as to reflexly lead to modifications in the way either of acceleration or retardation in the rate at which such gases were secreted or absorbed, and possibly in this way facilitate the more rapid adjustment of the volume of internal gas to the varying pressures of different depths. That the secretion of gas, and possibly its absorption also, are under the control of the nervous system has been experimentally proved by MOREAU in certain Physoclisti, but the absence of retia mirabilia in the Ostariophyseæ seems to us conclusive against assigning more than a very subordinate part to the mechanism, if any, in the way of controlling the secretion or absorption of gas in the latter group. On the other hand, it seems to us more reasonable to suppose that the Weberian mechanism controls the escape of gas through the ductus pneumaticus in the process of pressure adjustment during slow or rapid ascent. A gradual distension of the air-bladder would be accurately measured by its recording lever, the Weberian ossicles, and the increasing intensity of the stimulus imparted to the sensory epithelium of the internal ear and the saccular branches of the auditory nerve. The consequent reflex or voluntary efferent impulses may find expression in the exercise of some form of regulatory control over the liberation of gas through the ductus pneumaticus, so that only so much gas will be eliminated as will suffice to maintain the Fish in a plane of least effort at all levels during ascent, notwithstanding the reduction of external hydrostatic pressure. In a brief reference to this point RAMSAY WRIGHT (43) says that in Physostomous Fishes "accommodation to a new higher level is more quickly effected by the ejection of bubbles of gas through the air-duct," and again, in referring to the Ostariophyseæ, remarks that the Weberian mechanism "probably enables them to measure the precise amount of air which must be disengaged in order to restore equilibrium at a new higher level" (pp. 385–6). For reasons which we shall refer to subsequently, we cannot at present regard the first suggestion as applicable to the Physostomi in general, but, in so far as the Ostariophyseæ are concerned both suggestions agree with the tentative conclusions at which we also have arrived.

Unfortunately there is but little anatomical, and absolutely no experimental, evidence available as to how, or in what way, the escape of gas through the ductus pneumaticus is regulated or controlled in accordance with these conclusions. That the escape is in some way regulated is suggested by the fact that in the case of a Tench* under artificially diminished pressure the air issued from the ductus in the form of bubbles, not continuously, but at intervals, as the pressure was gradually reduced. The intermittent escape of the gas certainly seems to indicate the existence of some obstacle to what would otherwise be a continuous and gradual evolution of gas, and also suggests the presence of some check or regulating mechanism which periodically limited the outflow in accordance with the requirements of a gradually diminishing pressure, and thereby enabled the animal to retain a constant plane of least effort, for even in a partially exhausted air-pump the Fish still swam about freely. On this point RAMSAY WRIGHT (43) remarks, "the mode in which the air is discharged in *Amiurus* is not known to me, but the duct, tortuous where it opens into the œsophagus, must be much straighter when the ventral wall of the anterior part of the air-bladder is distended than when such is not the case. Further investigation must show whether the duct participates actively in disengaging the air-bubbles, and if so, under the control of what nerve it does so" (p. 386). We cannot altogether agree with RAMSAY WRIGHT'S suggestion that the escape of air from a distended air-bladder may be facilitated by the straightening of a tortuous pneumatic duct, for, as we have elsewhere shown, the skeletal attachments of the anterior chamber are such that it has but little capacity for distension except through the outward bulging of its lateral walls, in which the ventral wall can scarcely, if at all, participate. Nevertheless, we are strongly inclined to agree with his suggestion that the ductus pneumaticus does actively participate in promoting the escape of gas and in controlling the rate of exit, and on this point some clue as to the nature of the process may be gained by a comparison of substantially similar mechanisms in other organs with certain facts of structure in connection with the air-bladder and pneumatic duct of the Siluridæ, but their truth or falsity only experimental inquiry can determine.

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* MOREAU, *loc. cit.*

Comparative physiology furnishes many illustrations of the various methods by which the escape of partially solid or wholly fluid substances from the body, or from the organs, in which they are formed or temporarily stored, is regulated. A special sphincter muscle may surround the terminal outlet and be maintained in a normal condition of tonic contraction by impulses from a special nerve centre, the activity of which may be increased or inhibited by afferent impulses generated by appropriate external or internal stimuli. The sphincter ani may be taken as an example of this form of regulatory mechanism. Much more to the point, however, is the method by which the flow of bile from the gall-bladder to the small intestine in Mammalia is controlled. Both the cystic duct and the gall-bladder have muscular walls, while the terminal orifice of the common bile duct is said to be surrounded by a sphincter muscle. The relaxation of this sphincter and the contraction of the muscular walls of the gall-bladder and its duct may be brought about by a reflex action, in which the afferent impulses are due to the stimulus afforded by the passage of the acid contents of the stomach over the intestinal orifice of the bile duct, but nothing appears to be satisfactorily known either as to the nerve centre or to the path of the afferent impulses. It is clear that two distinct results follow the application of the stimulus and the initiation of afferent impulses, first, the inhibition of the centre by which the tonic contraction of this sphincter is maintained, and secondly, the contraction of the walls of the duct and gall-bladder. The cystic duct in Man is always somewhat tortuous at its commencement, and this may furnish an explanation of the fact that very considerable manual pressure is required to expel the contents of the gall-bladder, at all events, after death, and at the same time suggests that the muscular contraction by which the bile is normally expelled is of a gradual and peristaltic character. Moreover, the tortuosity of the cystic duct may have some physiological significance in the sense that it acts as a valve and prevents mere abdominal pressure from producing a flow of bile into the intestine.

The air-bladder and pneumatic duct certainly exhibit some structural analogies to the gall-bladder and cystic duct, and it is by no means improbable that a close physiological parallelism may also exist with regard to the expulsion of their respective contents. It is true that the walls of the air-bladder are devoid of both intrinsic and extrinsic muscles, and they can have no power of expelling the gases they enclose by direct muscular compression, but muscular action is here unnecessary, inasmuch as the augmented tension and volume of the contained gases under diminished pressure will furnish the needful expulsive force. Mere manual pressure on the air-bladder has but little, if any, effect in expelling its gaseous contents, and that this is so is probably due to the tortuosity of the pneumatic duct, aided possibly by the action of a terminal sphincter, at or near its gastric or œsophageal extremity. On the other hand, the ductus pneumaticus in some Siluridæ, and possibly in all the normal species, contains unstriped muscular fibres. The reflex mechanism in the two cases may also be similar. Diminished hydrostatic pressure conditions an expansion of the volume of gas in the air-bladder, which will ultimately result in the transmission of a stimulus to the sensory epithelium of the internal ear, and the initiation of afferent impulses in the auditory nerve. The afferent impulses may find their final expression in the peristaltic contraction of the walls of the pneumatic duct and the expulsion in successive bubbles of an amount of air that will suffice to restore equilibrium at a new level. It is probable that the pneumatic duct is not to be regarded as a mere channel for the escape of gas from the air-bladder, but rather as a structure which, under reflex control, actively participates in the process, and, at the same time, regulates the quantity of the expelled air. Slight reductions of pressure, the result of equally slight variations of level, may not necessarily lead to an escape of air, for probably no inconvenience to the locomotion of the Fish would result from them, in fact, the tortuosity of the pneumatic duct, aided, it may be, by a special sphincter, can be regarded as of the nature of a safeguard to prevent the unnecessary elimination of gas under such conditions. But more extensive reductions of pressure may at once call into play the reflex mechanism to secure the necessary readjustment to the more superficial level. That the reflex mechanism is under the direct control of some special nerve centre is highly probable, and it is at least within the range of possibility that the activity of this centre may in turn be dominated by some still higher centre whereby the processes involved in re-adjustment to constantly varying external pressures are brought under the voluntary control of the Fish.

A little additional light may, perhaps, be thrown on the nature of the regulatory mechanism by some remarks of DUFOSSÉ (11B). This writer describes the ductus pneumaticus in certain Ostariophyseæ, such as the Carp (*Cyprinus carpio*), the Barbel (*C. barbatus*), and the Miller's Thumb (*Cobitis barbatula*, LINN.) among the Cyprinidæ, as widening out into a trumpet-shaped orifice as it opens into the œsophagus, and that in this dilated part of the duct the mucous membrane presents several small duplicatures, which form valves so disposed as to prevent the exit of gas, the will of the animal and not the mere accumulation of gas being indispensable to overcome the valvular obstruction. DUFOSSÉ, however, regards these valves as forming a regulatory mechanism controlling the escape of air from the air-bladder by which these Fishes are rendered capable of producing certain voluntary sounds classified by him under the name of breathing noises, or "bruits de soufflement." In the absence of experimental evidence that such valves are related solely to the production of voluntary sounds, as DUFOSSÉ believes, it may not be altogether unreasonable to suggest that these structures may have something to do with regulating the expulsion of gas from the air-bladder under the influence of reduced hydrostatic pressure, and further that the breathing noises may only be the accidental concomitants of the latter function. At any rate, the existence of valvular structures in the ductus pneumaticus of, at all events, some few Ostariophyseæ affords an additional clue to the nature of the mechanism by which such Fishes may voluntarily or reflexly control the escape of air from the air-bladder.

Whatever may be the precise nature of the regulatory mechanism, the advantage to the Fish of some such method of carefully graduated adjustment to pressure variations as that we have suggested is sufficiently obvious. Without any kind of regulatory control, and with an open ductus pneumaticus in free communication with the exterior, it may be surmised that the escape of gas would be continuous and unchecked, and might even involve a more or less complete exhaustion of the gas in the air-bladder as the pressure diminished, with the contingent disadvantage that the normal equilibrium of the Fish in the water would be greatly disturbed, and a considerable demand be made on the secretive activity of the bladder for the subsequent restoration of the gas. On the other hand, the existence of a controlling mechanism would ensure that only so much gas would be evolved under such circumstances as might suffice to maintain the Fish in a plane of least effort, and at the same time secure the needful economy in the liberation of the gas.

There is another point of view from which, if the foregoing suggestions have any weight, the Weberian mechanism must be a source of considerable gain to all Fishes in which it is present. There can scarcely be any doubt that *all* Fishes, whether with or without this mechanism, must in ordinary locomotor movements encounter more or less extensive changes of level and pressure, although no doubt within limits which vary with different species. A Fish without the mechanism relies solely upon the relatively slow processes of gaseous secretion and absorption for the readjustment of the volume of gases contained within its air-bladder to pressure variations, and for reasons already given we have arrived at the conclusion that such processes are of little value in ordinary locomotor movements involving rapid changes of level and pressure, although possibly of considerable advantage when such changes are incurred in the course of periodic or other migrations. It will follow, therefore, that in ordinary locomotor movements attended by rapid changes of level any departure from the normal plane of equilibrium must be accompanied by an increase or decrease of specific gravity to an extent proportional to the amount of the pressure variation. Hence in all such movements a corresponding increase of muscular exertion must take place which will necessarily be the greater in proportion as the variation of level carries the Fish away from its normal plane of least effort, and the result is the same whether the Fish has to counteract by muscular effort the effect of a too feeble specific gravity, or to sustain itself against an increase of specific gravity. On the contrary, all Fishes that have a Weberian mechanism possess also a greater capacity for pressure adjustment, and consequently at nearly all levels and pressures will retain a normal plane of least effort, with the correlative advantage that all their normal movements, however rapid, and whatever may be the plane in which they take place, will be executed with a minimum expenditure of muscular energy. We may fairly conclude, therefore, that the Weberian mechanism not only confers upon all Fishes that possess it an exceptional capacity for freedom of locomotion in all directions, and especially in the vertical plane, but also entails the contingent advantage that all movements will be effected with the maximum economy of muscular effort and tissue metabolism.

This seems to be about as far as the data at present at our disposal will warrant us in pursuing this discussion as to the function of the Weberian mechanism. The evidence at present obtainable is strongly in favour of the presumption that this singular mechanism is directly related to the hydrostatic function of the air-bladder; nevertheless, we cannot but feel that the tentative suggestions which we have ventured to make as to its precise utility, while by no means inconsistent with them, yet derive but little positive support from any morphological or experimental data at present known. We have ventured to discuss this question at some length in order that the issues involved may be clearly understood, and in the hope that it will receive the attention of the experimental physiologist, in whose hands the final solution of the problem must rest.

So far our remarks have been confined to the discussion of the methods by which pressure adjustment is effected in the Physoclisti and Ostariophyseæ, and there still remain for consideration a few Physostomi (*e.g.*, Clupeidæ, Salmonidæ, Murænidæ, &c.), in which the air-bladder is said to be provided with an open ductus pneumaticus, but has no Weberian mechanism, and in which retia mirabilia are either present or wanting.* Two questions are suggested by these Fishes: (1) Are they capable, like the Ostariophyseæ, of utilizing the ductus pneumaticus as a means of pressure adjustment? (2) If so, what disadvantage is entailed upon them by the want of a Weberian mechanism? A negative answer to the first question renders any further discussion unnecessary, inasmuch as the Fishes concerned will be in the same position as most Physoclisti so far as pressure adjustment is concerned, but an affirmative response, on the contrary, will necessarily involve the consideration of the second question. With regard to the first point the scanty evidence available is of a contradictory character, in fact, it is not at all clear in many cases how far the ductus pneumaticus admits of free communication between the air-bladder and the exterior, in one species only, *Muræna conger* [*Conger vulgaris*], has it been experimentally shown† that gas can be eliminated through the pneumatic duct when the Fish is exposed to artificially diminished pressure. On the other hand, the Salmonidæ are generally credited with the possession of an open duct, but the behaviour of one species of this family, the "Kilch," when drawn to the surface from deep water scarcely favours the supposition that any adjustment to reduced pressure by the mechanical liberation of gas can take place in this species. It is true that in this case the pressure reduction was considerable, although it can hardly be said to have occurred with exceptional rapidity, or at a greater rate than probably takes place in many Ostariophyseæ during ordinary locomotion. Moreover, in MOREAU's experiments with such Ostariophyseæ as the Carp and Tench, the Fishes were exposed to an artificial reduction of pressure, which, if not so great as in the case of the "Kilch," was at least considerable and rapid, and yet throughout the experiment the gradual liberation of successive bubbles of gas enabled the Fish to retain perfect freedom of swimming. It is therefore difficult to avoid the conclusion that the "Kilch" has either no open pneumatic duct, or, if it has, that the duct cannot be utilized for pressure adjustment. A further item of negative evidence is to be found in the fact that, while retia mirabilia are invariably wanting in all Ostariophyseæ, they are present or absent in the remaining Physostomi in much the same way, and to the same extent, that they are present or wanting in the Physoclisti, and this certainly suggests the inference that gaseous secretion and absorption are important factors in pressure adjustment in these Fishes. From the same point of view it is somewhat significant that wherever the mechanical liberation of gas has been proved to take place in Fishes other than the Ostariophyseæ it is, with one exception (*e.g.*, *Conger*), by some other and secondarily acquired means than the retention of the ductus pneumaticus for the purpose. Thus MOREAU has shown that the Physoclist *Caranx trachurus* is capable of liberating a continuous stream of air through its "canal de sûreté" when exposed to artificially diminished pressures. In the light of such contradictory and mutually destructive evidence no satisfactory conclusion seems possible, but two alternative suggestions may be made. If the ductus pneumaticus cannot from any cause or other be used for the mechanical liberation of gas, then, in these Fishes, as in the typical Physoclisti, gaseous secretion and absorption must be the only methods of pressure adjustment. On the other hand, even if it be admitted that some Physostomi without WEBER'S mechanism can liberate gas through the pneumatic duct, it is nevertheless not difficult to see how it may be that the process is of little use to them for pressure adjustment. The completeness of the control exercised over the liberation of the necessary amount of gas will largely depend on the perfection of the reflex mechanism employed in the process, and in all the Fishes now under consideration the necessary afferent impulses must be initiated in the general peripheral nervous system by the diffused pressure exerted by a distended air-bladder on the surrounding organs, instead of in a particular afferent nerve by a stimulus applied to a localized sensory epithelium through a highly specialized arrangement of movable ossicles as is the case with the Ostariophyseæ. The indefinite character of the stimulus in the former would certainly militate against any delicacy in the process of adjustment, even if it did not altogether prevent the possibility of any such adjustment. The more perfect afferent mechanism of the Ostariophyseæ conditions a more effective control over the function of the pneumatic duct, and a greater capacity for regulating the processes involved in pressure adjustment, and it may also be that this is the precise advantage which the Weberian mechanism confers upon all Fishes that possess it.

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* A few Physoclisti (*e.g.*, *Holocentrum*, *Priacanthus*, *Cæsio*, &c.), in which, on the authority of KUER (21), an open ductus pneumaticus is present, may also be included.

† MOREAU, *loc. cit.*

It may be admitted that this suggestion does not necessarily preclude the possible use of the duct as a safety valve in certain cases, but it does negative the probability that any effective control can be exercised over the liberation of gas in ordinary locomotion.

We cannot conclude this section of our paper without remarking that it would be extremely interesting to compare the behaviour of a Physostomous Fish without a Weberian mechanism with one in which this mechanism is present, when exposed both to rapid and gradual variations of pressure. A careful and experimental comparison of the methods and rate of adjustment in the two types under such conditions should go a long way towards the discovery of the true function and utility of the Weberian apparatus.

There yet remain certain points in connection with the air-bladder of the Siluridæ which it is desirable should be discussed from a physiological point of view; these are (*a*) the lateral cutaneous areas; (*b*) the "elastic-spring" apparatus of MÜLLER; (*c*) the extrinsic muscles of the Pimelodinæ; and (*d*) the distinctive features of the air-bladder and Weberian mechanism in the Siluridæ as compared with other Ostariophyseæ.

(*a*.) *The lateral cutaneous areas.*—The close relation between the lateral walls of the anterior chamber of the air-bladder and the adjacent superficial skin, which is so characteristic of all the Siluridæ normales, and as equally conspicuous by its absence in all other Ostariophyseæ, may possibly have some physiological significance. SAGEMEHL (*loc. cit.*) has already referred to this feature in certain Siluroids, and suggests that, physiologically, it enables certain advantages to be realized, which, in other Ostariophyseæ, are gained by the bipartite structure of the air-bladder. In referring to the two-chambered air-bladders of the Cyprinidæ, Characinidæ, and the Gymnotidæ, he directs attention to the fact that this subdivision of the air-bladder occurs in no other Teleostei, and is always associated with the presence of a Weberian mechanism. The variable ratios of pressure of the surrounding medium condition the increase or decrease of the volume of gas contained in the whole air-bladder, and, owing to the peculiar structure of that organ, these variations of volume will find their expression almost exclusively in corresponding oscillations in volume of the small elastic anterior chamber, to which alone the Weberian ossicles are related, the larger posterior sac being scarcely, if at all, affected. A similar bipartition, the same writer also remarks, occurs only in a few Siluridæ, among which are mentioned, apparently on the authority of VALENCIENNES, *Auchenoglanis** and *Auchenipterus*. But in the case of the latter family SAGEMEHL says that the same physiological result is arrived at in an entirely different way. In many Ariinæ, and also in such Siluridæ as *Callichrous*, *Cryptopterus*, and *Schilbe*, the air-bladder is not confined to the abdominal cavity proper, but its lateral portions extend outwards between the ventral and dorsal portions of the lateral trunk muscles, quite close to the external skin. In this manner, SAGEMEHL remarks, the air-bladder acquires a tolerably direct connection with the external medium, and will, therefore, much more promptly react to pressure oscillations than if entirely confined to the abdominal cavity.

SAGEMEHL is scarcely correct in attributing any important physiological distinction between the obviously bipartite air-bladders of the Cyprinidæ and the Characinidæ and the air-bladders of the normal Siluridæ. In both cases the air-bladder is physiologically two-chambered in the sense that it consists of a smaller distensible anterior portion and a larger posterior and indistensible part, but in the Cyprinidæ the bipartite character is obvious externally, whereas in the Siluridæ it is only by internal examination that the essentially bipartite nature of the air-bladder becomes obvious. In fact, in all the normal Siluridæ the air-bladder is, physiologically, as truly bipartite as in other Ostariophyseæ, and the former derive precisely the same physiological advantage in the registration of hydrostatic pressure variations from this fact as do the latter. Neither is SAGEMEHL quite accurate in supposing that *Auchenoglanis** and *Auchenipterus* possess an air-bladder which is bipartite externally as in the Cyprinidæ, inasmuch as we have already shown, in the morphological section of this paper, that in both genera the bladder is substantially similar to that of all other Siluridæ normales so far as this point is concerned. SAGEMEHL's suggestion that the close relation of the lateral walls of the air-bladder to the external skin, and therefore to the surrounding medium, enables the air-bladder more promptly to react to pressure oscillations is, perhaps, not improbable, and, if such be the case, would certainly have the effect of rendering the Siluridæ much more sensitive to variations of hydrostatic pressure than is the case with other Ostariophyseæ where the air-bladder is separated from the external skin by the lateral lobes of the liver and other abdominal viscera. While admitting the feasibility of this suggestion, we may point out that the connection of the air-bladder with the superficial skin would also enable variations in the size of the air-bladder, the result of pressure variations, more promptly to modify the volume and specific gravity of the Fish, for any expansion or contraction of that organ from such causes must at once lead to the inward or outward bulging of the lateral cutaneous areas. The special advantage of lateral cutaneous areas to these Fishes, from this point of view, would lie in the fact that their greater susceptibility to alterations of volume and specific gravity would probably ensure a corresponding increase in the delicacy of the responsive processes involved in pressure adjustment.

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* *Auchenaspis*, BLEEK.

The possibility, however remote, that these anatomical features have no special physiological value, but are simply the necessary result of other structural modifications of undoubted utility, must also be kept in view. The relative shortness of the abdominal cavity in many Siluroids may have caused the lateral expansion of the air-bladder and its consequent abutment against the external skin. That this may be the case is suggested by the practical suppression of the lateral cutaneous areas in some Siluridæ (*e.g.*, *Malapterurus*) where the abdominal cavity is of greater relative length than usual. One of the conditions of the formation of lateral cutaneous areas, viz., the dorsal deflection of the dorso-lateral trunk muscles, may be only a necessary consequence of the elongation and expansion of the transverse processes of the fourth and fifth vertebræ, and their disposition at right angles to the long axis of the vertebral column for the investment of the dorsal wall of the anterior division of the air-bladder. In the Cyprinidæ, where lateral cutaneous areas are wanting, the transverse processes of the fourth vertebra are of considerable length without being specially expanded, but, like true ribs, their marked ventral flexure prevents them interrupting the straightforward course of the lateral trunk musculature, or producing any upward deflection of the dorso-lateral muscles. If this alternative view is at all a reasonable one, it will follow that the existence of the areas will primarily depend on the investment of the dorsal surface of the anterior chamber by the expanded transverse processes, which in turn must be regarded as a contrivance for preventing the dorsal expansion of the chamber during pressure variations, thereby restricting such alterations of volume to movements of the lateral walls alone.

(*b*.) *The "Elastic-spring" Apparatus.*—In the great majority of the Ostariophyseæ the escape of air from the air-bladder through the ductus pneumaticus apparently takes place only as the result of the expansion of the contained gases under the influence of diminished hydrostatic pressure, although it is possible that the rate of overflow may in some way be regulated. In some few Siluridæ, however, there does seem to exist a special mechanism by which, under certain conditions, the air-bladder may be subjected to considerable compression, and the air which it contains either forcibly expelled, or greatly reduced in volume by condensation. This mechanism presents two important modifications, viz., the "elastic spring apparatus" and the powerful extrinsic muscles of the Pimelodinæ. In the case of the "elastic spring apparatus" it would seem that by the contraction of its powerful protractor muscle each spring can be drawn forwards towards the head, while the subsequent relaxation of the muscle will at once enable the spring to exert its full pressure on the air-bladder. JOHANNES MÜLLER regarded this apparatus as a mechanism through which the condensation or rarefaction of the gases in the air-bladder became a motive force in causing the Fish to rise or fall in the water. On this view it is presumed that the contraction of the protractor muscles will pull forwards the anterior wall of the air-bladder to which the elastic springs are attached, and by that means lead to the expansion of the bladder and the rarefaction of its contained gases; while, on the contrary, the relaxation of the muscles will at once allow the springs, by their own elasticity, to compress the air-bladder, condense the gases within it, and consequently increase the specific gravity of the Fish. As MÜLLER remarks, condensation and rarefaction are placed under the action of two powerful and opposite forces, in such a manner that condensation results from the elasticity of a recoil, while rarefaction depends upon the action and persistence of an essentially muscular force which annihilates the recoil.

We cannot quite agree with MÜLLER that the elastic springs can have any share in dilating the air-bladder, or rarefying the gases which it contains. The bony plates in which the two springs terminate distally are only applied to the anterior wall of the air-bladder, and the fibres of the latter are not directly attached to, or inserted into, the plates at their points of contact, and it is, therefore, difficult to see how the forward movement of each spring can possibly draw the antero-lateral wall with it, or rarefy the contained gases by increasing the internal capacity of the air-bladder. It is quite true that the transverse membrane which is so closely applied to the anterior wall of the bladder is also continuous with the inner (or anterior) and ventral margins of the terminal long plates, but we have never been able to detect any connection between the latter and the component fibres of the tunica externa of the antero-lateral regions of the bladder itself. But even if it be true that the antero-lateral walls can be drawn forwards in the way which MÜLLER'S theory requires, it still seems to us extremely doubtful that any increase of internal capacity would necessarily result, inasmuch as any outward bulging in the antero-lateral regions would almost certainly be attended by an inward bulging elsewhere. The mobility and elasticity of the transverse process which forms each spring will certainly give to the lateral portions of the anterior wall that capacity for sharing in the distension of the anterior chamber which is prevented in all other Siluridæ by the absolute rigidity of the processes in question, but it is at the same time equally clear that the "elastic spring" apparatus cannot possibly give the Fish any power of directly compressing the air-bladder, except under certain conditions, viz., when the anterior chamber becomes distended through the diminution of pressure which occurs in movements of ascent, coincidently with the forward movement of the two springs as the result of the voluntary or reflex contraction of their protractor muscles. Under such circumstances the mechanism potentially acquires the power to modify the capacity of the air-bladder, for the subsequent relaxation of the muscles will at once enable the springs, through the force of their own recoil, to exert their full strength in compressing both the air-bladder and its gaseous contents.* If, therefore, the elastic springs can have no share in promoting ascent by rarefaction, and can only be called into action under conditions in which the distension of the air-bladder from pressure reduction is a necessary factor, the possibility that the mechanism is related to pressure adjustment is at once suggested. Tentatively adopting this suggestion it would seem that two alternative views may be taken as to the precise mode in which this singular mechanism is of practical utility :—

(1.) That the compression of the air-bladder, under the conditions and by the means already indicated, will effectually aid the action of the ductus pneumaticus in producing a more rapid and forcible ejection of gas, and at the same time secure the more rapid readjustment of the Fish to the reduced pressure of a more superficial level.

(2.) The advantage of a more rapid readjustment to diminished pressure may be gained by means of the "elastic spring apparatus" without necessarily involving a mechanical liberation of gas. The mere compression of the air-bladder would seem to be perfectly competent to prevent over-distension under a diminishing external pressure by simply condensing the contained gases, and so counteract the possible evil results of a too low specific gravity. If it be admitted that the Ostariophyseæ can control, or, if need be and occasion requires, entirely prevent the escape of gas through the pneumatic duct, it may easily be the case that pressure adjustment in those Siluridæ with an "elastic spring" mechanism can be more readily brought about by condensation without the actual expulsion of gas.

The sole advantage of the first alternative method is that it will secure a more rapid adjustment during ascent than is probably the case in most other Ostariophyseæ; on the other hand we incline to the opinion that the augmented tension of the gas itself under such conditions will constitute a sufficient expulsive force and render any special mechanism for the purpose altogether superfluous. The more obvious value of the second alternative lies in the fact that, while it may prove to be a method of adjustment even more rapid than the first, it also possesses the contingent economical advantage that as no gas has been lost by mechanical liberation, there will be no demand on the activity of the walls of the air-bladder for the secretion of additional gas when the Fish returns to a deeper level and greater pressure. On this view the processes of pressure adjustment will not consist in the actual expulsion of gas and its subsequent slow replacement by secretion, but rather in the volumetric changes of a fairly constant quantity of gas, which are affected by the action of the "elastic spring" apparatus, and are always of the opposite character to those which the external hydrostatic pressure tends to produce. Of the two alternatives the second seems to us the more feasible, but experiment alone can determine the accuracy of either, while it may prove the falsity of both.

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* Should this view of the mode of action of the "elastic spring" apparatus prove correct, it will be difficult to see how the mechanism can have anything to do with the production of voluntary sounds, as suggested by SÖRENSEN (36), inasmuch as the Fish would only be able to exercise its vocal powers under conditions involving pressure reduction during ascent from a deeper to a more superficial level. Under such conditions only does it seem likely that the contained gases would be expelled with sufficient force to produce any definite or characteristic sounds.

In a limited sense our second suggestion is in accordance with MÜLLER's theory, at least to the extent that condensation may be produced by the action of the elastic springs, although, as we think, for a different purpose than that which the theory maintains, but his view that the mechanism enables the Fish to ascend through the rarefaction of the contained gases must, for the reasons previously given, be regarded as entirely without foundation, and, to say the least, it is extremely doubtful if condensation can be of much, if any, use in facilitating descent. But apart from the special objections to the theory there are others of a more general character, based on the apparent uselessness of any special mechanism for causing the rise or fall of the Fish in the water. It has been previously pointed out that to Fish in approximate equilibrium the slightest action of the ordinary locomotor organs is quite sufficient to produce either ascent or descent, and the existence of an elaborate mechanism for varying the internal capacity of the air-bladder and the volume of the enclosed gases with this object is altogether unnecessary. These objections to MÜLLER's theory will apply with equal force whether it be presumed that condensation, or the actual expulsion of gas, is the prime agent in promoting descent. On the other hand the unquestionable importance to the Fish of rapid and accurate methods of pressure adjustment is highly suggestive that the "elastic spring" mechanism is solely related to this function. We prefer, therefore, to regard the mechanism as a contrivance for expediting the process of pressure adjustment when the Fish is exposed to a rapid reduction of pressure during quick ascent, which, far more than descent, necessitates both rapidity and accuracy in the readjustment processes, and this view may reasonably be adapted whichever of the two alternatives is accepted as to the precise method employed. Should our views on this point prove to be correct, it would be reasonable to anticipate that of all the Ostariophyseæ these Siluridæ are best qualified for rapid and extensive vertical locomotion under conditions the most favourable to the retention of perfect equilibrium at all levels within the range of their normal movements.

(*c.*) *The Extrinsic Muscles of the Air-bladder in the Pimelodinæ.*—A function substantially similar to that of the "elastic spring" apparatus may, in all probability, be assigned to the powerful compressor muscles of the Pimelodinæ. These muscles cannot possibly have any share in dilating the air-bladder and rarefying the contained gases in order to facilitate ascent, but it would certainly seem that they enable these particular Siluridæ to exercise a still more effective control over its distension, inasmuch as the muscles are apparently able to compress the air-bladder at all times, although more effectively, no doubt, when the latter is more or less distended. By the contraction of these muscles during rapid movements of ascent the tendency to over-distension on the part of the air-bladder will be promptly counteracted, while a forcible expulsion of gas through the pneumatic duct would enable the Fish to speedily adjust its volume and specific gravity to a new plane of least effort at the more superficial level. As in the case of the "elastic spring" apparatus of other Siluridæ, it is of course possible, theoretically, that the special advantage of the compressor muscles may be realised without necessarily involving the mechanical liberation of gas from the air-bladder. Excessive distension may be guarded against, and pressure adjustment effected by compression alone, the contained gases being so far condensed that no harmful reduction of the specific gravity of the Fish can take place, and, as before, accuracy and rapidity of pressure adjustment would, by this method, be correlated with the further advantage of economy in gaseous secretion.

In both series of Fishes it is extremely interesting to recall the existence of a special arrangement by means of which the compression of the air-bladder, either by the action of the "elastic springs," or by the contraction of special compressor muscles, is prevented from imparting a too violent shock to the Weberian mechanism, and more especially to the fluids and sensory epithelia of the internal ear. In the Pimelodinæ the contraction of the muscle which we have named the tensor tripodis, taking place coincidently with that of the compressor muscles, will effectually limit the violent excursions of the crescentic process of each tripus, which, otherwise, would certainly take place when the anterior chamber of the air-bladder is forcibly compressed in the way described. In those Siluridæ provided with the "elastic spring" mechanism, a precisely similar result is brought about by the existence of a groove at the junction of each terminal bony plate with its flexible and elastic root, into which the outer margin of the crescentic process of the tripus is received. During the compression of the anterior chamber by the "elastic springs," the outward movement of the crescentic process is controlled by the inward movement of the elastic spring itself, which has the result of effectually checking any sudden or extensive excursion on the part of the tripus, and, at the same time, prevents the transmission of a too violent impulse to the Weberian ossicles and internal ear.

The extreme difficulty of attempting to arrive at a satisfactory solution of the various problems arising out of the physiology of the air-bladder, through anatomical data alone, is again forcibly illustrated, for it is impossible entirely to exclude the possible relation of the extrinsic muscles of the Pimelodinæ to the function of sound production, and it may also be the case, although perhaps less likely, that the same reservation will also apply to the "elastic spring" mechanism. That a violent expulsion of air from the air-bladder should produce definite sounds is extremely probable, but how far such sounds can be considered as related to the primary function of these muscles, or as merely accidental concomitants to it, must for the present remain an open question. SÖRENSEN (36) has adopted the former suggestion, and regards both the compressor muscles and the "elastic spring" mechanism as being subordinate to sound production. Nevertheless, in the absence of confirmatory experimental evidence, we still think it worth while to direct attention to an alternative interpretation of the function of these structures, which is at least as consistent with their morphology as any other view at present suggested. We have elsewhere (p. 270 and p. 298) suggested certain difficulties, which, in our opinion, are serious objections to SÖRENSEN'S views on this point.

(*d.*) *The Siluridæ compared with other Ostariophyseæ.*—In our morphological summary, and elsewhere, we have drawn attention to the more salient features wherein the air-bladder and Weberian mechanism of the Siluridæ differ from the corresponding structures in those Ostariophyseæ which in these, as in other respects, are the most closely allied to them, viz.:—the Cyprinidæ, and we may now briefly consider such distinctions from a purely physiological standpoint. As the morphological result of a comparison of the two families was to demonstrate the increased specialisation of these structures in the Siluridæ it is highly probable that a similar comparison, from a functional point of view, will prove the increased sensitiveness of the latter to hydrostatic pressure variations, and, at the same time, suggest a corresponding advance in the accuracy of the readjustment processes. An important factor in this direction in the Siluridæ is the restriction of all variations in the capacity of the anterior chamber under the influence of pressure variations to lateral expansion or contraction, from which it must follow that the auditory organ will be rendered susceptible to smaller variations of pressure than is the case in the Cyprinidæ where expansion and contraction are less strictly localised, and probably take place to a nearly equal extent in all directions. To the same object must also be attributed the subdivision of the posterior section of the air-bladder in all normal Siluridæ into two lateral compartments by a vertical longitudinal septum, as well as the frequent presence of secondary transverse septa in each chamber, such structural features can scarcely have any other effect than that of rendering this portion of the air-bladder more inelastic and indistensible than it would otherwise be, and, therefore, still further restricting all volumetric variations to the anterior chamber alone. It is also possible that the presence of lateral cutaneous areas may be related to the increasing sensitiveness of the air-bladder of the Siluridæ to pressure disturbances, if, as

SAGEMEHL (*loc. cit.*) has suggested, the function of these areas is to enable the air-bladder more promptly to react to pressure oscillations, or, as we have surmised, more readily to allow variations in the volume of the contained gases to modify the bulk and specific gravity of the Fish.

The comparative freedom of the anterior vertebræ from anchylosis in the Cyprinidæ is obviously related to the fact that the air-bladder, including the anterior chamber, lies free in the abdominal cavity, and is scarcely, if at all, invested by skeletal elements; hence, as the bladder is less likely to be affected by any compression which may result from the flexure of the vertebral column during vigorous locomotor movements, anchylosis is unnecessary, or at all events does not take place to anything like the same extent as in the Siluridæ.

Certain distinctive structural variations in the Siluridæ are probably dependent upon other modifications of a more direct physiological value, and in any comparison with the Siluridæ it is interesting to notice the necessary sequence of particular anatomical differences between the two when an initial modification is once started in one of them. In the Siluridæ, the restriction of volumetric variations in the anterior chamber to its lateral expansion or contraction is in part brought about by the investment of its dorsal surface by the complex and fifth centra and the expanded and otherwise modified transverse processes of the fourth and fifth vertebræ, which not only prevents the expansion of the chamber dorsally, and to some extent anteriorly, but indirectly aids in preventing expansion in other directions by affording the necessary surface for the direct attachment of the walls of the chamber to the skeleton at certain definite points. But to prevent the flexure of the trunk vertebræ in ordinary locomotion from exerting any influence on an air-bladder so closely related to the skeleton, and secondarily on the Weberian ossicles, a more or less extensive anchylosis of the anterior vertebræ takes place, as well as a more rigid and intimate articulation with the skull than is usually the case in other Ostariophyseæ. The necessity for a more rigid connection between the skull and the vertebral column has probably conditioned further modifications in the anterior vertebræ, and may well have been one of the causes which have hastened the further atrophy of those rudimentary vertebral centra that intervene between the basioccipital and the fourth vertebra, and have been partially dismembered in the formation of the different Weberian ossicles from certain of their constituent elements. The shortening of this section of the vertebral column necessarily involves the tripus taking a position more anterior than that which it occupies in the Cyprinidæ and exactly opposite the scaphium, with the final result that the intercalarium becomes useless as a sesamoid ossicle, and degenerates to the insignificant and variably developed vestige by which alone it is represented in the great majority of the Siluridæ.

On the other hand, it is not easy to attach any precise physiological significance to the fact that the saccus paravertebralis in the Siluridæ has entirely lost that communication with the cranial cavity which it possesses in the Cyprinidæ, nor to certain minor differences in the degree of development and the mutual relations of the different Weberian ossicles in the two families. Perhaps the most important difference is the removal of the two claustra from any obvious physiological relations with the atrial cavities in the Siluridæ, and it is by no means clear whether this should be regarded as a loss or a gain from a physiological point of view.

Of the remaining families of the Ostariophyseæ the Characinidæ closely resemble the Cyprinidæ in so far as the points now under discussion are concerned, and of the Gymnotidæ it may be said that they exhibit a somewhat less specialized condition of the air-bladder and Weberian ossicles than any of the preceding families, although obviously related to the Cyprinoid type.

The conclusion suggested by these facts seems to us to be this—that, physiologically considered, the most important distinctive features of the Weberian mechanism in the Siluridæ as compared with other Ostariophyseæ are mainly related to the air-bladder, which in the former attains its maximum degree of specialization as an organ adapted for the registration of varying hydrostatic pressures.

B. *Siluridæ abnormales.*

In considering, from a physiological point of view, the significance of the structural modifications presented by the air-bladder and its adjuncts in this section of the family, we may, in the first place, briefly capitulate certain anatomical facts already mentioned in a previous section of this paper.

Apart from a very considerable reduction, both in absolute and relative size, the absence of lateral chambers and the persistence of the anterior chamber only, the most noteworthy features in the air-bladder of the various genera of Siluridæ abnormales are—its constriction, partial or complete, into two laterally-situated air-sacs, which may not only lose all connection with each other, but with the œsophagus also; the tendency of the air-sacs to become more or less completely enclosed within variously-formed bony capsules; the occasional atrophy of the ductus pneumaticus, or its persistence as a solid fibrous cord; and frequently also, in addition, the more or less complete atrophy of the fibres which normally form the dorsal walls of lateral halves of the bladder, and connect the lateral walls with the crescentic processes of the tripodes. To these may be added the partial solidification of the organ in certain species, either through the thickening and matting together of its walls, or the development of internal fibrous trabeculæ, or through the partial obliteration of its cavity through the growth of a thick central column of fibres. With the exception of the intercalaria, which are often absent, without, however, in any way interfering with the complete anatomical connection of the tripodes with the scaphia and the claustra, which apparently have no functional significance in the Siluridæ, the remaining Weberian ossicles are fairly well developed, and retain their normal relative size. Traces of degeneration are, however, to be met with. The tripus generally loses its characteristic crescentic curvature—a modification which is often associated with the more or less complete atrophy of the fibres that normally converge to this ossicle from the lateral walls of the air-bladder, and even when these fibres are present the loss of curvature may be due to the fact that reduction in the size of the bladder is not accompanied by a corresponding diminution in the size of the tripus itself, which, therefore, receives the insertion of fewer fibres than in most Siluridæ normales. The scaphium as frequently retains but a vestige or loses all trace of its ascending process, and, as the condylar process may also disappear, the ossicle often becomes reduced to the condition of a simple concavo-convex structure in relation with the external atrial aperture.

As regards the effects of degeneration of the air-bladder on the structure of those portions of the internal ear which are specially related to the Weberian ossicles, we are satisfied that in, at least, some Siluridæ abnormales the sinus endolymphaticus has completely disappeared, although the ductus endolymphaticus, the cavum sinus imparis, and the atrial cavities remain, and retain also their normal relations to one another and to the scaphia. The absence of a sinus endolymphaticus in several genera with rudimentary air-bladders is at least suggestive of the probability that it is also wanting in other Siluroids in which the air-bladder has undergone a like degeneration; on the other hand, we entertain no doubt as to the presence of an apparently functional sinus in a few Siluridæ abnormales. Physiologically, the suppression of the sinus endolymphaticus must prove a serious obstacle to the transmission of afferent impulses generated by varying external pressures to the sensory epithelium of the sacculi, even supposing that the air-bladder and Weberian ossicles still retained their normal structure and mutual relations; but that it is a fatal obstacle cannot, in our opinion, be so readily affirmed, for movements in the fluids of the atrial cavities and cavum sinus imparis might still impinge on that portion of the ductus endolymphaticus which is in relation with the anterior aperture of the cavum.

Even if the diminutive air-bladder of the Siluridæ abnormales retained its structural integrity in other respects, the almost universal atrophy of the lateral chambers would certainly have the effect of rendering the bladder far less delicate as a register of varying hydrostatic pressures than it is in the normal section of the family, but taken in conjunction with such other retrogressive changes both in the air-bladder and Weberian mechanism as those above mentioned, it becomes almost impossible to believe that any function of the kind suggested can be assigned to these structures, or that they do otherwise than present various stages of retrogressive modification towards the condition of vestigial and functionless organs; and this conclusion seems to us equally inevitable whatever may have been their original function—whether acoustic, barometrical, or hydrostatic. Considering the high degree of specialisation which characterises the air-bladder and Weberian mechanism in the Siluridæ, it is by no means surprising that these structures should be liable to rapid degeneration when from any cause the necessity for the exercise of their special function no longer exists, and the extraordinary variations which they often exhibit in different Siluridæ abnormales can only be regarded as furnishing abundant illustrations of the extreme variability to which all degenerate and useless organs are liable.

The widespread degeneracy of the air-bladder in the Siluridæ is amply proved by the fact that of the one hundred and sixteen genera mentioned in the British Museum Catalogue of the family, no fewer than twenty-five are referable to the Siluridæ abnormales, and it is extremely probable that further investigation, especially among the various mailed Loricaroid forms and their naked allies, will considerably add to the number of Siluridæ with degenerate and functionless air-bladders.

The causes that have led to the degeneracy of the air-bladder in so many forms are in many instances not difficult to trace, and, as in so many Physoclist Teleostei, the assumption of a purely ground habit of life is probably the most important one. Not a few of the genera of Siluridæ abnormales inhabit the comparatively shallow waters of rapidly flowing mountain streams and torrents, often living at a considerable altitude, and in general habit are not unlike our common English Loaches. Many are provided with an adhesive apparatus on the ventral surface of the body between the pectoral fins for attachment to stones, so that they may be enabled to withstand the force of mountain torrents. Such Fishes when not in motion by the exercise of their fins probably rest upon, or attach themselves to, the river bottom, and the utter uselessness and probable harmfulness of an air-bladder as a hydrostatic organ under such conditions is no doubt the cause of its degenerate and rudimentary condition in such Siluroids as *Sisor*, *Pseudecheneis*, *Glyptosternum*, *Euclyptosternum*, *Exostoma*, *Amblyceps*, &c. Although very different from the latter in the character of their habitat a similar explanation will probably apply also to such widely dissimilar forms as *Callichthys* and *Clarias*. Various species of *Callichthys* are said* to keep under plants in marshy swamps, to be able to burrow in the mud, in which they often become dried up, and even to be capable of migration upon land in search of water. On the same authority *Clarias magur* is said to often frequent ponds and ditches, and, when the water dries up, to become imbedded in the mud, where it sojourns until the advent of the next rainy season. The same species is said to possess exceptional vitality when removed from its natural habitat. From their partially amphibious and grovelling habits it is clear that an air-bladder can be of little use to these Fishes as a hydrostatic organ, and hence its rudimentary condition. Similar remarks will in all probability apply to such other *Clarias*-like forms as *Saccobranchus* and *Heterobranchus*, and probably also to many other Loricaroid types in addition to *Callichthys*, about which we have not been able to glean much positive information as to their habits. The position of the mouth and the retroverted and Loach-like character of the lips in so many Loricaroid genera is strongly suggestive of their grovelling habits, and the consequent uselessness of an air-bladder.

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* CUVIER et VALENCIENNES (8), vol. 15, pp. 219–220; also p. 228.

With reference to one of these forms* WEYENBERGH (40, pp. 91, 92), remarks that from its "ground" habitat and peculiar shape an air-bladder is unnecessary and consequently has entirely atrophied. WEYENBERGH's statement that the air-bladder is absent in this species is certainly inaccurate, since the results of REISSNER's investigations, which we are able to confirm, have demonstrated its existence in a rudimentary condition, but his remarks as to the uselessness of the organ in the light of the peculiar habits of the fish are worthy of note.

But although it is possible in the case of many Siluridæ abnormales to prove the association of a "ground" habit with the possession of a rudimentary air-bladder in the probable relation of cause and effect, there are a few genera in which this is much more difficult. *Bagarius, Silondia, Ailia, Eutropiichthys* and *Callomystax* are neither inhabitants of mountain streams or torrents, nor are they in any sense amphibious, but, on the contrary, frequent the larger rivers of the low country and plains of India, and beyond this we have not been able to obtain any precise information as to their habitat or mode of life. The non-utility of the air-bladder as a hydrostatic organ in several of these Siluroids is very obvious from its extremely small size, and notably in *Bagarius Yarrellii,* where each of the two air-sacs into which the bladder is divided was only equal to the size of a garden pea in a Fish weighing ten pounds. In all such instances as these we can only suggest that here, as in many other cases, it is highly probable that the rudimentary condition of the air-bladder will eventually be found to be correlated with a purely ground life. Hence, it may be concluded that in the case of many Siluridæ abnormales there is a certain amount of evidence which strongly favours the view that the degenerate condition of the air-bladder is directly caused by reversion to a "ground" life, and also that, by analogy, this is likewise true of the remaining species and genera where, from ignorance of their habits, no trustworthy evidence on this point can at present be obtained. If our contention should ultimately prove to be correct, it will furnish a strong argument in favour of the conclusion which, on other grounds, we have already arrived at, viz., that the Weberian mechanism is physiologically related to the normal hydrostatic function of the air-bladder, and not to audition, or to the perception of varying atmospheric pressures.

The susceptibility of the air-bladder to change of habitat on the part of its possessor is well shown by the variations which occur within the limits of the same genus. Two species of *Cryptopterus* (*C. micropus* and *C. hexapterus*) have rudimentary air-bladders, while all the remaining species of the genus that came under our notice had those organs unusually well-developed. The genus *Pimelodus* exhibits an even more interesting illustration of the influence of a change of habit on the condition of the air-bladder. In two species of this genus (*P. pulcher* and *P. sapo*) the air-bladder itself is not only rudimentary but lacks even a trace of the compressor and tensor tripodis muscles which are so characteristic of the normal Pimelodinæ.

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* *Hypostomus plecostomus*, CUV. et VAL. = *Plecostomus bicirrhosus*, GRONOV.

In the absence of any definite knowledge of the habits of these species no certain conclusions can be drawn as to the causes which have brought about the rudimentary state of the air-bladder, but the assumption of a "ground" habit may prove to be one of them.

The structural variations met with in the air-bladder of different Siluridæ abnormales require, in many instances, no special explanation, and are readily explicable as being due to the more or less complete degeneration of parts of a useless organ, combined with the usual polymorphism of vestigial structures. Such features as the diminutive size of the air-bladder; the atrophy of the lateral compartments and the partial solidification of the reduced anterior chamber; the atrophy of the fibrous tracts by which the contraction or distension of the air-bladder becomes converted into corresponding movements of the Weberian ossicles; and the suppression of the ductus pneumaticus, can be easily understood as having arisen in this way. But there are nevertheless at least two features in connection with the air-bladder, which are somewhat difficult to explain. One is, its persistence even in a reduced condition, when as a useless organ its total suppression would seem to be the more natural result, and indeed is the only result so far as all other Teleostei are concerned, while the second difficulty is the partial or complete encapsulation of the vestigial air-bladder by bone. The following considerations may possibly throw some light on the first of these difficulties:—

The degeneration of an organ which, from change of habit, has become more or less useless to its possessor may be brought about by the single or conjoint operation of several causes. (1) The cessation of the preservative influence of natural selection, or what WEISMANN has termed "panmyxia," combined with what GALTON has called "regression towards mediocrity," so that the organ fails to be maintained at its previous high level of development. (2) Reduction in size and simplification in other respects of a useless organ may also be due to action of natural selection in view of the advantage which the animal derives from economy of nutrition. (3) The retention in its fully developed condition of an organ of no functional utility might entail some positive disadvantage to the animal when exposed to new conditions of life, in which case the operation of natural selection in more or less completely eliminating the useless structure would be certain and speedy. On the assumption of a "ground" habit by a Fish, the air-bladder would tend to become useless and, sooner or later, vestigial, and it is highly probable that the three factors mentioned above may all have co-operated in initiating this result. But like so many other vestigial structures, and especially those which result from the retrogressive modification of organs of great functional importance in a large series of animals, and therefore probably of great antiquity, the air-bladder, even when useless, often exhibits a singular vitality and persistence. The initial degeneration of the air-bladder in its useless condition may be accounted for, in part, by the advantage of economy of nutrition; but reduction in size beyond a certain limit can scarcely have been due to this cause alone, for long before its total disappearance the nutritive requirements of the organ must become so infinitesimally small that no positive or obvious disadvantage could result from its retention in a diminutive condition. When extrinsic muscles in connection with the air-bladder become useless, economy of nutrition would, no doubt, soon lead to the total suppression of such highly vascular structures, and hence the complete atrophy of the compressor and tensor tripodis muscles of certain Pimelodinæ with rudimentary air-bladders is, on the contrary, easy to understand. Then again, while it is by no means difficult to see that the persistence of a fully developed air-bladder in purely "ground" Fishes might not only be useless, but even positively harmful, when the animal habitually rests on the bottom when not in motion by the exercise of its fins, it is at the same time difficult to appreciate the disadvantage of retaining an air-bladder so small as to be utterly without influence in its locomotor functions, or in any way capable of imparting undue buoyancy to the animal. Hence it seems to us, of the three causes tending to produce degeneration, the only ones likely to have much effect in reducing the air-bladder beyond a certain minimum size are "panmyxia" and "regression towards mediocrity," and it may therefore be conjectured that the antagonistic force of heredity has so far retarded the operation of these causes as to have secured the persistence of a small vestigial air-bladder in all existing Siluridæ abnormales. A difficulty in the way of this explanation of the invariable retention of a small vestigial and useless air-bladder in these Siluroids instead of its total suppression is the fact that in so many Teleostei, where the air-bladder has presumably become useless from some cause or other, the total disappearance of the organ follows almost as a matter of course. In certain families, Physostomi and Physoclisti, the air-bladder is totally absent. The Scopelidæ and Symbranchidæ are examples of this in the former group, and the Pleuronectidæ and Lophiidæ in the latter; and if the line of argument adopted above in the special case of the Siluridæ has any force, it would be reasonable to anticipate that it would also apply to the former, and that in these families a small vestigial, even if useless, air-bladder would be very generally present, which, as a matter of fact, is never the case. The suppression of an organ so physiologically important as the air-bladder in entire families of Teleostei is, of course, suggestive that the operation of causes tending to produce this result has probably extended over a far wider period of time than has been the case with genera or species only of those Siluroids in which merely a partial reduction has taken place, and that given sufficient time, and the accumulative action of such causes, the same ultimate result would be arrived at in the latter as in the former. But in opposition to this suggestion must be placed the fact that in certain Physoclist families (*e.g.*, Scombridæ and Polynemidæ) the air-bladder is absent in some species of the same genus while present in others. Thus, on the authority of DAY,* it is stated that *Scomber colias* possesses an air-bladder, while *S. scomber* has none; similarly among the Asiatic species of *Polynemus*, *P. paradiseus* and *P. tetradactylus* are without air-bladders, while, on the contrary, such organs are present in *P. indicus* and *P. plebejus*. Such facts certainly seem to indicate that total suppression may take place so rapidly as to have become completed within the relatively limited time that has elapsed since certain of these Fishes acquired their present specific characters. Without attempting to assign relative values to the three causes which have probably brought about the total atrophy of the air-bladder in these instances, the evidence seems strongly in favour of the view that, either singly or conjointly, their operation is calculated to lead to the speedy and complete suppression of a useless air-bladder, and is distinctly adverse to the retention of that organ, however vestigial may be the condition to which it has been reduced; hence the persistence of a vestigial air-bladder in so many Siluridæ, in spite of causes which, in most other Fishes, have sufficed to secure its total atrophy, can hardly be explained by the suggestion previously made by us.

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* "The Burbot (*Lota vulgaris*) and Air-Bladder of Fishes," 'Cotteswold Nat. Field Club,' 1880.

The widespread persistency of a vestigial and useless air-bladder seems to be peculiar to the Ostariophyseæ; in fact, we know of no species in any of the different families of the group in which an air-bladder is entirely wanting. On the contrary, so far as our knowledge extends, this fact is altogether without parallel in all the remaining families of Teleostei, in which total suppression seems invariably to follow loss of function. There are, however, two points in connection with the air-bladder of the Siluridæ abnormales that are not without some significance, and may possibly furnish an explanation of this anomaly. The first has reference to the method by which the reduction of the bladder has been effected. We have previously pointed out that the vestigial air-bladder in these Siluroids represents the anterior chamber only of the normally developed organ, and that the lateral compartments have almost always undergone total atrophy. The process of reduction has, therefore, not affected all parts of the air-bladder to an equal extent, and, while it has almost invariably led to the total suppression of all trace of lateral chambers, the anterior chamber has been allowed to persist in a reduced and vestigial condition; or in other words, while total atrophy has taken place with respect to that part of the bladder not specially related to the Weberian ossicles, that portion of it which alone is directly connected with those ossicles invariably persists. The second point relates to the persistence of the now useless Weberian ossicles. The uniform retention of a fairly complete series of ossicles in all Siluridæ abnormales is explicable as due to the absence of any potent cause for their speedy suppression. Economy of nutrition can have scarcely any effect in this direction, nor need the direct action of natural selection be invoked for the purpose, for, if useless, their persistence need not necessarily prove a source of disadvantage or harm to their possessor. Whatever trace of degeneration the mechanism presents may therefore be solely due to "panmyxia," or to "regression towards mediocrity," and these, as we have already conjectured, are causes that operate with extreme slowness. The conclusion suggested to us by these facts, and one which seems to offer a reasonable explanation of what would otherwise be a singular anomaly, is this: that the curious and, in many respects, unique persistence of a useless air-bladder is due to its highly specialized connection with the Weberian mechanism. As is well known, comparative anatomy affords numerous examples of the persistence of functionless but harmless skeletal structures, which occasionally may even retain traces of their softer connections, and, in our opinion, it is the retention of the Weberian ossicles that has been the principal cause of the persistence of a useless air-bladder, in much the same way that the useless and rudimentary bones of the hind limbs of certain aquatic Mammalia sometimes retain remnants of their equally useless muscles and ligaments.

The second problem suggested, viz., the frequent encapsulation of the rudimentary air-bladder by bone in abnormal Siluridæ, is a very difficult one, and one which we must confess our inability to explain satisfactorily, or to do more than suggest possible solutions. Three points may be kept in view in discussing this question:—(1) That the degree of encapsulation generally bears some relation to the extent to which the air-bladder retains the structural integrity of its walls and its apparently normal connection with the tripodes;* (2) that however defective in some respects the individual Weberian ossicles may be, the continuity of those that persist is complete in all Siluridæ abnormales; and (3) that encapsulation is strictly confined to the rudimentary air-bladders of the Ostariophyseæ, and occurs in no other living Teleostei.†

Partial encapsulation, to the extent that the reduced air-bladder occupies transversely disposed grooves or hollows on the ventral surfaces of the expanded and conjoined transverse processes of the fourth and fifth vertebræ, is, perhaps, not difficult to explain, for reduction in the size of the anterior chamber has simply been accompanied by a corresponding contraction and curvature of the modified transverse processes which normally closely invest and are adapted to the convexity of its dorsal and anterior surfaces. The difficulty is felt to be greater in the case of such Siluroids as *Cetopsis, Clarias, Callomystax, Acanthicus*, and the various Loricaroid genera, in which the diminutive air bladder is almost completely encapsuled by bone, and while obviously useless for all hydrostatic purposes, retains much of its structural integrity as well as its normal relations to the Weberian ossicles. In several of these genera, in addition to the share taken by the transverse processes, which of itself might be readily accounted for in the way suggested above, certain additional means are employed to ensure the more complete enclosure of the air-bladder within osseous capsules, and this at least suggests the possibility that some specific and useful object is to be gained thereby. Of these additional methods we may again refer to the partial ossification of the walls of the air-bladder itself (*e.g.*, *Acanthicus*), and to the development of special bony laminæ (ventral processes) by the extension of bony deposit from the superficial ossifications investing the complex centrum with the superficial fibrous tissue which lies between the peritoneum and the ventral surface of the bladder. In such cases as these it may be conjectured that the retention of even a rudimentary air-bladder would be harmful to its owner if it were even imperfectly in physiological connection with the auditory organ through the Weberian ossicles, for even a purely "ground" Fish may be exposed to variations of hydrostatic pressure in the course of its migrations at different depths, or over the uneven bed of a river, or, as might be the case in some instances, where the Fish inhabited tidal rivers, by the rise or fall of the tide, and such variations might lead to the transmission of stimuli to the auditory organ, but no responsive adjustment on the part of the Fish could take place on account of the utter uselessness of the air-bladder for its normal hydrostatic function. Physiologically, the enclosure of the reduced air-bladder within a bony capsule would have the effect of preventing its expansion under the influence of diminished pressure, and conceivably therefore subserve the purpose of preventing the transmission of useless and disturbing stimuli to the central nervous system.

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* See Morphological Summary, pp. 251, 252, and p. 259.

† According to WILLIAMSON (41) the air-bladder in certain fossil Ganoids has ossified walls. If it were possible it would be extremely interesting to ascertain if these fishes possessed any form of Weberian mechanism.

On the other hand, in several abnormal Siluroids (*e.g.*, *Bagarius*, *Akysis*, *Acrochordonichthys*, *Glyptosternum*, *Euclyptosternum*, &c.) the air-bladder has so far undergone retrogressive modification in one way or another as to have been structurally incapable of responding to variations of external pressure, or of initiating any movements in the chain of Weberian ossicles. In all these Siluroids the atrophy of the fibres forming the dorsal walls of the two lateral air-sacs constitutes a structural lesion so obvious that it is impossible that any alterations in the volume of the air-bladder could be converted into corresponding movements of the Weberian mechanism or in any way affect the auditory organ. In such instances complete encapsulation is, *ex hypothesi*, unnecessary, and therefore does not take place. As suggested above, the partial enclosure of the air-bladder within mere grooves or recesses on the ventral surfaces of the modified transverse processes may here be regarded as simply due to the fact that, as the organ lost its lateral compartments and the anterior chamber gradually became smaller, the transverse processes still continued to retain their normal relations to the latter, while at the same time contracting and more or less curving round it. On the other hand, there are one or two abnormal forms (*e.g.*, *Pimelodus pulcher* and *Schilbichthys*) in which encapsulation is but partial, although the structural integrity of the air-bladder is so far maintained that it might still be susceptible to slight volumetric changes when exposed to pressure variations, and also be able to convert such changes of volume into movements of the Weberian ossicles, but in these, and in one or two other similar cases, it will generally be found that the bladder is so far environed by bone that no lateral distension can take place. Thus in the types referred to the osseous grooves are contracted distally in such a way as to effectually check all tendency to lateral expansion on the part of the air-bladder. In *Schilbichthys* it will be noted that even the stem and inferior limb of the post-temporal may co-operate in securing this result.

We have ventured to suggest this explanation in those cases where encapsulation is most complete, because at first sight it seems to be a legitimate inference from the three facts to which reference has just been made, but as an objection it may be urged that the same physiological result might have been gained by simpler and more natural means. Complete or partial atrophy of the air-bladder would even more effectually have prevented transmission of useless stimuli to the auditory organ, and would seem also to be the more natural as well as the more easily acquired safeguard. In some cases (*e.g.*, *Bagarius, Glyptosternum,* &c.) the latter method apparently is the one adopted for the purpose. But if our previous conclusion, that the useless air-bladder owes its singular persistence in these Siluroids to its connection with the Weberian ossicles, be correct, it may nevertheless have happened that in other cases reduction in the size of the air-bladder took place so slowly that encapsulation superseded complete atrophy as a means for securing the object in question. It must also be borne in mind that even in its normal condition the air-bladder and its connective tissue investment are frequently invaded by ossified deposit. The superficial ossification of the complex centrum and the ventral processes, the terminal plates of the "elastic-spring" apparatus, and the posterior extremities of the tripodes, are examples of this tendency. More or less complete encapsulation through an extension of this process may therefore have been more readily acquired than at first sight would seem possible or probable.

If it be objected that this view is somewhat far-fetched, an alternative explanation of the difficulty may be suggested. It is possible that encapsulation has really no physiological significance. Whatever share the modified transverse processes take in the process may be only due to their tendency to contract round and envelope an atrophying structure to an extensive portion of the surface of which they are always closely moulded, while the development of such additional means of encapsulation as the ossification of the walls of the air-bladder itself, or the growth of ventral processes, is due solely to an exaggeration of that tendency to ossification which is always obvious in the normal air-bladder when no longer checked in the useless organ by the controlling influence of natural selection.

It is interesting to observe that other families of Ostariophyseæ, and notably those Cyprinidæ included in the sub-group Cobitidinæ, exhibit a parallel, and in many respects a substantially similar series of modifications. As WEBER (*loc. cit.*) first pointed out, the air-bladder of *Cobitis fossilis* is not only of relatively small size, but is also completely enclosed within a thin bony capsule of corresponding shape. Other Loach-like forms as, for example, *Nemachilus* and *Botia*, present the same peculiarity, and it is by no means improbable that a similarly modified air-bladder is present in all or most of the remaining genera of this section of the family. In the three genera mentioned above the degeneration and encapsulation of the air-bladder follow much the same lines as in the Siluridæ abnormales. The series of Weberian ossicles is complete, including even an intercalarium; the anterior chamber of the typically bilocular Cyprinoid air-bladder, as a rule, alone persists, although in a much reduced condition; the posterior chamber, if present at all, is scarcely more than the barest rudiment; and it is the anterior alone which is encapsuled by bone. Furthermore, such characteristic modifications of the air-bladder are, in these genera, undoubtedly associated with a purely ground habit of life. *Nemachilus barbatula*, the commonest of English Cobitidinæ, is unquestionably a ground Fish, its general habit being to lurk under stones at the bottom of rapidly-flowing streams, or, if nearer the surface, to rest on floating weeds. The popular names "Groundling" and "Stone Loach" sufficiently indicate the habits of this Fish. *Cobitis tænia*, a much rarer English species, is also a "ground" Fish, but it is said to be partial to muddy bottoms. Of the East Indian genus *Botia*, DAY* remarks that it "can scarcely be said to be entirely a ground feeder, but seems intermediate in habit between the true Carp and the grovelling Loaches." In the condition of its air-bladder *Botia* exhibits a similar gradation between the two types, for, while the anterior chamber is completely encapsuled by bone, the posterior chamber, though reduced in size, is still better developed than in *Cobitis* and *Nemachilus.*

So close a parallelism in the condition of the air-bladder and the habits of its possessor in two families so well defined and distinct, both in general characters and the structure of the air-bladder and Weberian mechanism, as the Cyprinidæ and Siluridæ, can only be due to the operation of similar causes in both instances, and in our opinion is strongly confirmatory of the conclusions we have already arrived at in the case of the latter family. But although the modifications which the air-bladder undergoes in the abnormal forms of both families are substantially similar in principle and in result, and have no doubt been evolved in each case to bring the organism into harmony with practically similar external conditions, there are certain minor differences between the two as to the precise means employed. Encapsulation of the air-bladder in the Cyprinidæ appears invariably to result from the actual ossification of the walls of the air-bladder itself, the modified transverse processes taking little, if any, share in the process. This may possibly be explained by the fact that in these Cyprinidæ with a normally-developed air-bladder, the transverse processes, though greatly developed in size and otherwise modified, are never so expanded or so closely moulded to the anterior and dorsal surfaces of the anterior chamber as is always the case in the normal Siluridæ, and hence, instead of encapsulation being effected, as is generally the case in the latter, by a slight extension of a modification already existing, it has been brought about in the former by the actual ossification of the outer coat of the air-bladder itself. The completeness of encapsulation in the Cyprinidæ we associate with the general integrity of the rest of the air-bladder and Weberian mechanism, for reasons previously urged in the case of certain Siluridæ abnormales. Further investigation may prove that a considerable number of Cyprinidæ besides the Cobitidinæ possess reduced and bone-encapsuled air-bladders, more especially those hilly or Alpine genera, such as *Gymnocypris*, *Oreinus*, *Schizothorax*, *Ptychobarbus*, *Schizopygopsis*, *Diptychus*, and others, that certainly live under conditions in every respect very similar to those which in so many Siluridæ are associated with a degenerate bladder. The small East Indian Cyprinidæ which are included in the sub-group Homalopterina are usually described as entirely without an air-bladder. They are said to be exclusively ground forms, with the ventral surface of the body flattened for adhesion to stones at the bottom of the rapid hill and mountain streams to which they are restricted. The habits of these Fishes would certainly lead us to expect that the air-bladder would be rudimentary and enclosed within bony capsules, but its complete suppression is unique so far as the Ostariophyseæ are concerned. But in view of the fact that the very existence of an air-bladder has been denied in the case of several Siluroids which are now known to possess at least a vestige of that organ, the statement that it is completely absent in the Homalopterinæ cannot be accepted without further confirmation.

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* 'Cotteswold Nat. Field Club,' 1880, p. 19.

VI.—CONCLUDING REMARKS.

The many and varied structural modifications met with in the air-bladder of the Siluridæ are not surprising in view of the exceptionally diversified conditions under which the different species and genera live. Their geographical distribution is almost co-extensive with the tropical and subtropical regions of the Earth's surface, and both the habitat and habits of the different species are remarkably varied. Some Alpine species are restricted to mountain streams often at an altitude of several thousands of feet above the sea level, and sometimes reaching a height of 15,000 feet, as is the case with certain Siluroids of the Andes of South America; other species are characteristic of the streams of the hilly country of a lower level; while other species again are equally characteristic of the larger rivers and lakes of the plains; and a limited few are marine, extending even to some of the Oceanic islands of the Pacific. The climatic variations to which the Siluridæ are subject are almost as diversified. Though mainly tropical or subtropical, certain genera are exposed to an almost Arctic climate, at least for a portion of the year, the result either of the altitude at which they live, or of their extension to the confines of the north temperate regions. The physical conditions under which many Siluridæ are capable of living are almost as varied as their geographical distribution or climatic range. Many of them are ground-feeders; some of them have a remarkable power of living out of water; others are liable through prolonged drought and the consequent drying up of rivers or lakes to become buried in the mud for longer or shorter periods without subsequent injury; and others again are said to be capable of migration upon land from river to river.

DARWIN* has pointed out, in referring to the conditions favourable to variation in animals and plants, that it is common, widely-diffused and widely-ranging species that vary most, and that this might be expected from the diverse physical conditions to which they are exposed, as well as from differences in the nature and quality of their living competitors in different regions. Elsewhere* he likewise alludes to the fact that an organ developed in an extraordinary manner implies that it is of high functional importance to the species, and that it may also be concluded that the organ has undergone a great amount of variation since it first came into existence. It is clear that the Siluridæ furnish an admirable illustration of the truth of these remarks. Their extensive geographical distribution and highly varied habitat, their richness alike in individuals and species, and, in short, their dominant position in fresh waters over wide areas, are quite sufficient to account for almost infinite variation. On the other hand, in the air-bladder and Weberian mechanism combined we have an organ, which, from its highly specialized and remarkable development, must be of great functional importance to these Fishes. Hence, the extraordinary variations which this organ and its correlated skeletal structures present need occasion no surprise when it is obvious that we have in the character of the organ itself, and in the external environment of the family in which it is most highly specialized, all the conditions necessary for the action of natural selection in producing rapid and extensive modification, either in the progressive or retrogressive direction. Under such conditions adequate scope would be afforded for the operation of natural selection in perfecting the useful organ and eliminating by atrophy and degeneration the useless one. Nor is it difficult to see how it is that the Weberian apparatus and air-bladder are more specialized in the Siluridæ than in other Ostariophyseæ. The only rivals to the Siluridæ in the extent of their geographical distribution are the Cyprinidæ, for the remaining families have but a comparatively restricted range. But extensive as is their geographical distribution, the great majority of the Cyprinidæ appear to exist under fairly uniform conditions, or, at all events, exhibit nothing like the diversity of habitat and habits that is so characteristic of the Siluridæ, and hence it is that so far as the structure of the air-bladder and Weberian mechanism is known in the former family, it presents but little variation in the direction of increased specialization, although in a few genera the effects of degeneration are sufficiently obvious.

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* 'The Origin of Species,' 6th ed., pp. 42 to 43.

VII.—Systematic Index.

In this Index we have adhered to Dr. Günther's classification and order of enumeration, as set forth in his "Catalogue of the Fishes in the British Museum," vol. 5, 1864, p. xi. Species referred to by us which are not in that Catalogue are added at the end of the list of species belonging to that particular genus. The pages where any species is described in detail are indicated by the use of a heavier type.

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* *Ibid.*, p. 119.

Siluridæ.

First Sub-family. Siluridæ Homalopteræ.

First Group. Clariina.

Clarias, Gronov.
    anguillaris, L., 188, **195.**
    macracanthus, Gthr., **195.**
    magur, Ham. Buch., 187, 188, **195**, 305.
    fuscus, Lacép., 188, **195.**
    Nieuhofii, C. et V., **187–195**, 199.
    hasselquistii, C. et V., **187.**
Macropteronotus magur (cf. *Clarias*).
Heterobranchus, Geoffr., **195.**

Second Group. Plotosina.

Plotosus, Lacép.
    anguillaris, Bl., **197, 198.**
    canius, Ham. Buch., **195–197**, 198, 201.
Copidoglanis, Gthr.
    albilabris, C. et V., **198.**
Cnidoglanis, Gthr.
    megastoma, Richards, **198**, 201.

Third Group. Chacina.

Chaca, C. et V.
    lophioides, C. et V., **199.**

Second Sub-family. Siluridæ Heteropteræ.

Fourth Group. Silurina.

Saccobranchus, C. et V.
    fossilis, Bl., **199, 200.**
Silurus, Artedi.
    glanis, L., 66, 100, **200, 201**, 226, 233, 282.
    cochinchinensis, C. et V., **201.**
Wallago, Blkr.
    attu, Schn., **201.**
Eutropiichthys, Blkr.
    vacha, Ham. Buch., **201, 202.**

- *Cryptopterus*, Gthr.
  - *limpok*, Blkr., **203**, 213.
  - *palembangensis*, Blkr., **203**.
  - *bicirrhis*, C. et V., **203**.
  - *micropus*, Blkr., 202, **204**, **205**, 211, 249, 306.
  - *micronema*, Blkr., **202**, 203, 235.
  - *hexapterus*, Blkr., 202, 204, **205**, 249, 306.
  - *micropogon*, Blkr., **203**, 235.
- *Callichrous*, Gthr.
  - *bimaculatus*, Bl., **207**.
  - *ceylonensis*, Gthr., 202, **206**, **207**.
  - *pabo*, Ham. Buch., **207**.
  - *hypophthalmus*, Blkr., **207**.
- *Schilbe*, Blkr.
  - *mystius*, C. et V., **207**, **208**.
- *Eutropius*, Müll. et Trosch.
  - *niloticus*, Rüpp., **208**.
  - *murius* (cf. *Pseudeutropius*).
- *Ailia*, C. et V.
  - *bengalensis*, Gray, **208–211**.
- *Schilbichthys*, Blkr.
  - *garua*, Ham. Buch., 202, **211–213**, 214 (cf. *Pseudeutropius*).
- *Laïs*, Blkr.
  - *hexanema*, Blkr., **213**, **214**.
- *Pseudeutropius*, Blkr.
  - *atherinoides*, Bl., **214**.
  - *goongwaree*, Sykes, **214**.
  - *murius*, Ham. Buch., **214** (cf. *Eutropius*).
  - *garua* (cf. *Schilbichthys*).
- *Pangasius*, C. et V.
  - *Buchanani*, C. et V., 167, **214–218**, 219, 234, 235, 243, 244.
  - *djambal*, Blkr., 167, 214, **219**, 235, 243, 244.
  - *macronema*, Blkr., **219**, **220**, 221, 235, 243, 244.
  - *micronema*, Blkr., **220**, **221**, 244.
  - *juaro*, Blkr., **221**, 243, 244.
- *Silondia*, C. et V.
  - *gangetica*, C. et V., **221–223**.

Third Sub-family. SILURIDÆ ANOMALOPTERÆ.

Fifth Group. HYPOPHTHALMINA.

Hypophthalmus, C. et V.
  marginatus, C. et V., **176–178**.

Fourth Sub-family. SILURIDÆ PROTEROPTERÆ.

Sixth Group. BAGRINA.

Bagrus, BLKR.
  bayad, FORSK., **102**.
  docmac, FORSK., **102**.
  (*Sciades*) *emphysetus*, M. et T. (cf. *Arius*).
Chrysichthys, GTHR.
  macrops, GTHR., **102**.
Macrones, DUM.
  nigriceps, C. et V., **100**.
  aor, HAM. BUCH., 76, **101**, **102**, 103, 232, 235, 237, 243.
  gulio, HAM. BUCH., **100**.
  nemurus, C. et V., **63**, **100**, 101, 102, 103, 104, 106, 218, 240, 268, 275.
  Hoevenii, BLKR., **100**, **101**, 104.
  planiceps, K. et v. H., **100**.
  tengara, HAM. BUCH., **100**.
  Wolffii, BLKR., **100**.
  armatus, DAY (*M. vittatus*, BLKR.), **100**.
Pseudobagrus, BLKR.
  fulvi-draco, RICHARDS, **103**.
  brachysoma, GTHR., **102**, **103**, 105, 112.
Liocassis, BLKR.
  micropogon, BLKR., **103**, **104**.
Bagroides, BLKR.
  melanopterus, BLKR., 103, **104**, **105**, 235.
Rita, BLKR.
  crucigera, OWEN, **105–107**.
Acrochordonichthys, BLKR.
  pleurostigma, BLKR., 107, **110–112**.
Akysis, BLKR.
  variegatus, BLKR., **107–110**.
  Kurzii, DAY, **110**.

- *Olyra*, M'Clell.
  - *burmanica*, Day, **112**.
- *Amiurus*, Gthr.
  - *catus*, L., 66, 69, 78, 80, 98, 100, 130, **112**, 224, 233, 260, 267, 275.

Seventh Group. PIMELODINA.

- *Sorubim*, Blkr.
  - *lima*, Schn., **118**.
- *Platystoma*, Agass.
  - *fasciatum*, L., **118**, 125, 135, 246.
  - *tigrinum*, C. et V., **113–118**, 135, 243, 246.
  - *coruscans*, Agass., **118**, 246.
- *Piramutana*, Gthr.
  - *piramuta*, Kner., **118**, **119**, 243.
  - *Blochii*, C. et V., **119**.
- *Pseudarioides clarias*, Bl. (cf. *Piramutana Blochii*).
- *Piratinga*, Gthr.
  - *filamentosa*, Licht., **119**, 246.
- *Pimelodus*, Gthr.
  - *maculatus*, Lacép., **119**, **120**, 243.
  - *ornatus*, Kner., **120**, 243.
  - *sapo*, Val., **123–125**, 247, 248, 249, 253, 306.
  - *pulcher*, Boul., **121–123**, 248, 250, 253, 306, 311.
  - *pangasius*, Ham. Buch. (cf. *Pangasius Buchanani*).
  - *platypogon*, K. et v. H. (cf. *Glyptosternum*).
  - *filamentosa*, Licht. (cf. *Piratinga*).
  - *macropterus*, Licht. (cf. *Callophysus*).
- *Callophysus*, M. et T.
  - *macropterus*, Licht., **125**.
- *Auchenoglanis*, Gthr. (*Auchenaspis*, Blkr.)
  - *biscutatus*, Geoffr., 88, **125–127**.

Eighth Group. ARIINA.

- *Arius*, Gthr.
  - *thalassinus*, Rüpp., 137.
  - *sagor*, Ham. Buch., 137, **138**.
  - *arioides*, C. et V., 137.
  - *assimilis*, Gthr., 137, **138**.
  - *emphysetus*, M. et T., 139, 246.
  - *latiscutatus*, Gthr., 137, **138**.

Milberti, C. et V., 138, 246.
truncatus, C. et V., 137.
cœlatus, C. et V., 137, **138**, 246.
venosus, C. et V., 137, **138**.
utik, Blkr., 137.
argyropleuron, K. et v. H., 137.
maculatus, Thunb., 137.
pidada, Blkr., **128–137**, 139, 140, 141, 143, 154.
gagora, Ham. Buch., 138, 139.
australis, 137, **138**.
Hemipimelodus, Blkr.
borneensis, Blkr., **139**, **140**.
(*cenia*, Ham. Buch., **140**, = *Callomystax* sp.).
(*viridescens*, Ham. Buch., **140**, = *Callomystax* sp.).
Galeichthys Gronovii (cf. *Ælurichthys*).
Ketengus. Blkr.
typus, Blkr., **140**.
Ælurichthys, Baird et Gir.
longispinis, Gthr., **140**, 141, 246.
Gronovii, C. et V., **140**, **141**, 246.
Osteogeniosus, Blkr.
militaris, L., 143.
Valenciennesii, Blkr., **141–143**.
macrocephalus, Blkr., **143**.
Batrachocephalus, Blkr.
mino, Ham. Buch., 133, **141**.

Ninth Group. BAGARINA.

Bagarius, Blkr.
Yarrellii, Sykes, **143–147**, 187, 190, 306.
Euclyptosternum, Gthr.
sp. ? **155**.
Glyptosternum, Gthr.
platypogon, K. et v. H., **147–155**.
telchitta, Ham. Buch., 147.
conirostris, Steindach, **155**.
Hara, Blyth.
Buchanani, Blyth, **155**.
Amblyceps, Blyth.
sp. ? **156**.

Fifth Sub-family. SILURIDÆ STENOBRANCHIÆ.

Tenth Group. DORADINA.

- *Ageniosus*, LACÉP.
  - *militaris*, BL., **156**, 253, 259.
- *Euanemus*, M. et T.
  - *nuchalis*, SPIX, **162**, **163**.
- *Auchenipterus*, C. et V.
  - *nodosus*, BL., **156–162**, 165, 264.
  - *obscurus*, GTHR., **162**, 236, 264.
- *Cetopsis*, AGASS.
  - *candira*, AGASS, **163**, **164**.
- *Doras*, GTHR.
  - *maculatus*, VAL. (? *muricus*, KNER.), **164**, **165**, 246.
- *Oxydoras*, GTHR.
  - *brevis*, HECK., **165**, **166**, 244.
- *Synodontis*, C. et V.
  - *Schal*, SCHN., **166–168**.

Eleventh Group. RHINOGLANINA.

- *Callomystax*, GTHR.
  - *gagata*, HAM. BUCH., **168–173**, 139, 140.

Twelfth Group. MALAPTERURINA.

- *Malapterurus*, LACÉP.
  - *electricus*, GM., **173–176**, 235.
  - *beninensis*, MURRAY, **176**.

Sixth Sub-family. SILURIDÆ PROTEROPODES.

Thirteenth Group. HYPOSTOMATINA.

- *Callichthys*, L.
  - *asper*, Q. et G., **183**.
  - *littoralis*, HANCOCK, 178, 183.
- *Plecostomus*, GTHR. (*Hypostomus*, LACÉP.).
  - *verres*, C. et V., 178, **183**.
- *Acanthicus*, SPIX ("*Rhinelepis*").
  - *hystrix*, SPIX, **178–180**, 181, 182, 183.

Loricaria, L.
  cataphracta, L., 178, **180–182.**
  nudirostris, KNER, **180–182.**
Sisor, HAM. BUCH., 183.
Pseudecheneis, BLYTH, **183.**
Exostoma, BLYTH.
  Blythii, DAY, **184.**

Fourteenth Group. ASPREDININA.

Aspredo, L.
  batrachus, L. (*lævis*, BL.), 184.
  cotylophorus, BL., **184–187.**

VIII.—REFERENCES.

1. BAUDELOT, E.—"De la détermination des pièces osseuses qui se trouvent en rapport avec les premières vertèbres chez les Cyprins, les Loches et les Silures." 'Comptes Rendus,' vol. 66, 1868, p. 330.
2. BIOT.—'Mémoires de la Société d'Arcueil,' vol. 1, 1807.
3. BORELLI.—'De motu animalium,' Romæ, 1680; and Lugduni Batavorum, 1685.
4. BRIDGE, T. W.—"The Air-bladder in certain Siluroid Fishes." 'Birmingham Phil. Soc. Proc.,' vol. 6, 1888, p. 131.
5. BRIDGE and HADDON.—"Contributions to the Anatomy of Fishes, (I.) the Air-bladder and Weberian Ossicles in the Siluridæ." 'Roy. Soc. Proc.,' vol. 46, 1889, p. 309; (II.) *Ibid.*, vol. 52, 1892, p. 139.
6. CHARBONNEL-SALLE.—"Sur les fonctions hydrostatiques de la vessie natatoire." 'Comptes Rendus,' vol. 104, 1887, p. 1330.
6A. CLELAND, J.—"On the Skeleton, Muscles, and Viscera of *Malapterurus beninensis*." 'Edinb. New Phil. Journ.,' vol. 8 (N.S.), 1858, p. 177.
7. COPE, E. D.—"Observations on the Systematic Relations of the Fishes." 'American Naturalist,' 1871, p. 579; and 'Trans. Amer. Phil. Soc.,' vol. 14, 1871, p. 445.
8. CUVIER et VALENCIENNES.—'Histoire naturelle des Poissons,' 1828–1845, vol. 14, 1839; vol. 15, 1840.
9. DAY, FRANCIS.—"On the Freshwater Siluroids of India and Burmah." 'Zool. Soc. Proc.' (London), 1871, p. 703.
10. —— "Notes on Indian Siluroid Fishes.' 'Zool. Soc. Proc.' (London), 1871, p. 286.
10A. —— 'The Fishes of Great Britain and Ireland,' 1880–84, vol. 2.
11. DELAGE, YVES.—"Sur une fonction nouvelle des otocystes comme organe d'orientation locomotrice." 'Archives Zool. expér. et gén.,' 2 Sér., vol. 5, 1887. See also abstract in 'Journ. Roy. Microsc. Soc.,' 1887, pp. 52, 732.

11A. DELAROCHE, F.—"Observations sur la vessie aérienne des Poissons." 'Ann. du Mus. d'histoire naturelle,' vol. 14, 1809, p. 180.

11B. DUFOSSÉ.—"Recherches sur les bruits et les sons expressifs que font entendre les Poissons d'Europe, et sur les organes producteurs de ces phénomènes acoustiques." 'Ann. des Sci. Nat. (Zool.),' vol. 19, Art. No. 5, 1874.

12. ENGELMANN, W.—"Über die Function der Otolithen." 'Zool. Anzeig.,' vol. 10, 1887, p. 439; abstract in the 'Journ. Roy. Microsc. Soc.,' 1887, p. 938.

13. GILL, T.—"Arrangement of the families of Fishes." 'Smithsonian Miscellaneous Collections,' vol. 11, 1872.

13A. GOURIET, É.—"Du rôle de la vessie natatoire." 'Ann. des Sci. Nat. (Zool.),' vol. 6, 1866, p. 369.

14. GÜNTHER, A.—'Introduction to the Study of Fishes,' Edinburgh, 1880.

15. —— 'Catalogue of the Fishes in the British Museum,' vol. 5, 1864.

16. —— "Ichthyology." 'Encycl. Britann.,' ed. IX., vol. 12, 1881, p. 630.

17. GRASSI, B.—"Beiträge zur näheren Kenntnis der Entwicklung der Wirbelsäule der Teleostier." 'Morphol. Jahrb.,' vol. 8, 1883, p. 457.

17A. HADDON, A. C.—"On the Stridulating Apparatus of *Callomystax gagata.*" 'Journ. Anat. Phys.,' vol. 15, 1881, p. 322.

18. HASSE, C.—"Beobachtungen über die Schwimmblase der Fische." 'Anatomische Studien,' vol. 1, 1873, p. 583.

19. —— "Das Gehörorgan der Fische." 'Anatomische Studien,' vol. 1, 1873, p. 417.

20. JOBERT.—Quoted in SEMPER's 'Animal Life,' (34, p. 444.).

21. KNER, R.—"Einiges über die Thymusdrüse bei Fischen und die Schwimmblase der Stachelflosser. 'Sitz. Math.-Nat. Classe, Akad. Wissen., Wien,' vol. 49, 1864; p. 455.

22. LEYDIG.—'Lehrbuch der Histologie des Menschen und der Thiere,' Frankfort, 1857.

23. MCKENZIE, T., WRIGHT, R. RAMSAY, MCMURRICH, J. P., and MACULLUM, A. B. (43).

24. MACULLUM, A. B., WRIGHT, R. RAMSAY, MCMURRICH, J. P., and MCKENZIE, T. (43).

25. MILNE-EDWARDS, H.—'Leçons sur la Physiologie.' 1856–1862.

26. MONOYER.—"Recherches expérimentales sur l'équilibre et la locomotion chez les Poissons." 'Ann. des Sci. Nat.' (Zool.), vol. 6, 1866, p. 5.

27. MOREAU, A.—"Recherches expérimentales sur les fonctions de la vessie natatoire." 'Ann. des Sci. Nat.' (Zool.), vol. 4 (No. 8), 1876.

27A. —— "Sur la voix des Poissons." 'Comptes Rendus,' vol. 59, 1864, p. 436.

28. MÜLLER, JOHANNES.—"Untersuchungen über die Eingeweide der Fische. (iii.) Beobachtungen über die Schwimmblase der Fische." 'Abhandl. Akad. Berlin,' 1843 [1845], p. 135. Previously published in abstract in 'Monatsbericht Akad. Berlin,' 1842, and 'Archiv für Anat. und Phys.,' 1842, p. 306.

28A. MURRAY, A.—"Remarks on the Natural History of Electric Fishes, with the description of a new species of *Malapterurus* from the Old Calabar River, West Africa." 'Edin. New Phil. Jour.' (N.S.), vol. 2, 1855, p. 35.

29. NUSBAUM, J.—"Ueber das anatomische Verhältniss zwischen dem Gehörorgane und der Schwimmblase bei den Cyprinoiden." 'Zool. Anzeig.,' vol. 4, 1881, p. 552.

30. OWEN, R.—"On the Anatomy of Vertebrates," vol. 1. 'Fishes and Reptiles.' 1866.

31. PARKER, T. J.—"On the connection of the air-bladder and the auditory organ in the Red Cod (*Lotella bacchus*)." 'Trans. New Zealand Institute,' vol. 15, 1882, p. 234.

32. REISSNER.—"Ueber die Schwimmblase und den Gehörapparat einiger Siluroiden." 'Archiv. für Anatomie, Phys., und wiss. Medicin.' Leipzig, 1859, p. 421.

33. SAGEMEHL, M.—"Beiträge zur vergleichenden Anatomie der Fische. (iii.) Das Cranium der Characiniden nebst allgemeinen Bemerkungen über die mit einem Weber'schen Apparat versehenen Physostomenfamilien," 'Morphol. Jahrb.,' vol. 10, 1885, p. 1.

34. SEMPER, K.—"The Natural Conditions of Existence as they affect Animal Life." 'Internat. Scientific Series,' 1881.

35. ST. HILAIRE, G.—"Description de l'Egypte" (2), vol. 24.

36. SÖRENSEN, W.—'Om Lydorganer hos Fiske.' (Dissertation for Doctor's Degree.) Copenhagen, 1884.

37. —— 'Om Forbeninger i Svömmeblæren, Pleura og Aortas Væg og Sammensmeltung deraf med Hvirvelsöjlen særlig hos Siluroiderne samt de saakaldte Weberske Knoglers Morfologi.' 'Vidensk. Selsk. Skr., 6 Række, naturvidensk. og mathemat. Afd.,' VII. 2. Copenhagen, 1890, p. 67.

38. TAYLOR, J.—"On the Respiratory Organs and Air-bladder of certain Fishes of the Ganges." 'Edinburgh Journ. Science' (N.S.), vol. 5, 1831, p. 33.

39. WEBER, E. H.—"De aure et auditu hominis et animalium." Pars i. 'De aure animalium aquatilium.' Leipzig, 1820.

40. WEYENBERGH, H.—"*Hypostomus plecostomus*, Val. Mémoire anatomique pour servir à l'histoire naturelle des Loricaires." Cordoba, 1876.

41. WILLIAMSON, W. C.—"On the Microscopic Structure of the Scales and Dermal Teeth of some Ganoid and Placoid Fish." 'Phil. Trans.,' 1849, p. 435.

42. WRIGHT, R. RAMSAY.—"The Relationship between the Air-bladder and Auditory Organ in *Amiurus*." 'Zool. Anzeig.,' vol. 7, 1884, p. 248.

43. ——, MCMURRICH, J. P., MACULLUM, A. B., and MCKENZIE, T.—"Contributions to the Anatomy of *Amiurus*." Toronto, 1884. Reprinted from 'Proc. Canadian Institute' (N.S.), vol. 2, 1884, p. 251.

44. —— "On the Skull and Auditory Organ of the Siluroid *Hypophthalmus*." 'Canada, Roy. Soc. Trans.,' vol. 3, sect. iv., 1885, p. 107.

IX.—Description of the Plates.

(*Unless stated otherwise the Figures are of natural size. Figures relating to any species are not necessarily all drawn from the same specimen.*)

PLATE XI.

Figs. 1–6 and 8–24.—*Macrones nemurus.*

Fig. 1. Lateral view of the skull and anterior vertebræ.

Fig. 2. Vertical longitudinal section.

Fig. 3. Ventral view of hinder part of skull and the anterior vertebræ; × 2.

Fig. 4. Lateral view; × 3.

Fig. 5. Vertical longitudinal section of the hinder part of the skull, and of the first and complex vertebræ; × 3.

Fig. 6. Posterior face of the skull and the post-temporal of the left side; × $1\frac{1}{2}$.

Fig. 7. Transverse section through the occipital region of the skull of *Macrones aor*; × 2.

Fig. 8. View of the cranial floor and auditory capsules, the roof of the skull having been removed; × 3.

Fig. 9. A similar view, but with the membranous labyrinth *in situ*, so as to show the relations of the latter to the Weberian ossicles; semi-diagrammatic; × 4.

Fig. 10. The Weberian ossicles; external lateral view, × 3.

Fig. 11. The scaphium; internal view; × 3.

Fig. 12. The Weberian ossicles; ventral view; × 3.

Fig. 13. The tripus; dorsal view; × 3.

Fig. 14. The tripus; ventral view; × 3.

PLATE XII.

Fig. 15. Lateral view of the head and anterior portion of the trunk.

Fig. 16. Lateral view of the head and anterior portion of the trunk, after the removal of the external skin on the right side.

Fig. 17. Ventral view of the air-bladder *in situ*; × 2.

Fig. 18. Ventral view of the air-bladder *in situ*; after the removal of its ventral wall; × 2.

Fig. 19. The dorsal and lateral walls of the air-bladder, showing the arrangement of the fibres forming the outer and inner strata of the tunica externa; their relations to the tripodes, and the anterior

and posterior pillars of the anterior chamber; semi-diagrammatic; × 2.

Fig. 20. Similar view of part of the dorsal wall of the anterior chamber; × 4.

Fig. 21. Weberian ossicles; ventral view, showing the attachment of the fibres of the inner stratum of the tunica externa to the left tripus, and also the radial fibres; × 3.

Fig. 22. Similar view of the attachment of the fibres of the outer stratum; × 3.

Fig. 23. Transverse section through the body in the region of the anterior chamber of the air-bladder; semi-diagrammatic.

Fig. 24. Diagrammatic representation of the relations of the auditory organ, the cavum sinus imparis, and the atrial cavities to the Weberian ossicles and air-bladder.

Fig. 25.—*Macrones aor.* View of the posterior face of the skull with the post-temporals *in situ.*

PLATE XIII.

Fig. 26.—*Pseudobagrus brachysoma.* Ventral view of the anterior vertebræ and the modified transverse processes.

Fig. 27.—*Rita crucigera.* Ventral view of the cavity of the air-bladder.

Fig. 28.—*Acrochordonichthys pleurostigma.* Base of the skull, and the modified anterior vertebræ; ventral view; × 3.

Figs. 29 and 30.—*Akysis variegatus.*

Fig. 29. Base of the skull, and the anterior vertebræ; ventral view; × 2.

Fig. 30. Ventral view of the air-sacs *in situ;* × 3.

Figs. 31–34.—*Platystoma tigrinum.*

Fig. 31. Vertical longitudinal section through the anterior vertebræ; ½ nat. size.

Fig. 32. Ventral view of the left halves of the anterior vertebræ and their processes; ½ nat. size.

Fig. 33. Ventral view of the air-bladder *in situ.*

Fig. 34. Interior of the air-bladder; ventral view.

PLATE XIV.

Fig. 35.—*Piramutana piramuta.* Ventral view of the base of the skull and of the anterior vertebræ; the interior of the right half of the bladder is also shown; × 2.

Fig. 36.—*Pimelodus ornatus.* Interior of the air-bladder; ventral view; × 2.

Figs. 37, 38.—*Pimelodus sapo.*

Fig. 37. Ventral view of the right half of the bladder and the left osseous capsule; the ventral part of the right capsule has been removed; × 1½.

Fig. 38. The left tripus; ventral view; × 3.

Figs. 39–41.—*Pimelodus pulcher.*

Fig. 39. Base of the skull, the right air-sac, the left osseous capsule, and the modified anterior vertebræ; × 2.

Fig. 40. Ventral view of the interior of the two air-sacs; × 2.

Fig. 41. Ventral view of the left tripus; × 2.

Figs. 42–44.—*Auchenoglanis biscutatus.*

Fig. 42. Ventral view of the right halves of the anterior vertebræ and their processes.

Fig. 43. The left tripus; ventral view.

Fig. 44. Ventral view of the interior of the air-bladder.

Figs. 45–49.—*Arius pidada.*

Fig. 45. Lateral view of the hinder part of the skull and the anterior vertebræ.

PLATE XV.

Fig. 46. Vertical longitudinal section of the hinder part of the skull and the anterior vertebræ.

Fig. 47. The base of the skull and the anterior vertebræ; ventral view.

Fig. 48. Interior of the air-bladder; ventral view.

Fig. 49. The Weberian ossicles.

Fig. 50.—*Ketengus typus.* Lateral view of the interior of the air-bladder, the right outer wall having been removed.

Fig. 51.—*Osteogeniosus Valenciennesii.* Ventral view of the interior of the air-bladder.

Fig. 52.—*Batrachocephalus mino.* Interior of the air-bladder; ventral view.

Figs. 53, 54.—*Bagarius Yarrellii.*

Fig. 53. The base of the skull, the anterior vertebræ, the right air-sac, and the left osseous capsule. The stem and ascending process of the post temporal have been removed; × 2.

Fig. 54. The left tripus; × 2.

PLATE XVI.

Figs. 55–58.—*Glyptosternum platypogon.*

Fig. 55. The base of the skull, the anterior vertebræ, and the bony capsules for the air-sacs; ventral view; × 2.

Fig. 56. Lateral view of the hinder part of the skull, the pectoral girdle, and the neural spines of the anterior vertebræ; × 2.

Fig. 57. Ventral view of the two air-sacs, showing their relations to the osseous capsules; × 2.

Fig. 58. The right tripus; × 2.

Figs. 59–63.—*Auchenipterus nodosus.*

Fig. 59. Ventral view of the anterior vertebræ and the "elastic-spring" apparatus.

Fig. 60. Similar view of the interior of the air-bladder.

Fig. 61. Lateral view of the air-bladder and skull, showing the left protractor muscle of the mechanism.

Fig. 62. Ventral view of the right tripus.

Fig. 63. Dorsal view.

Figs. 64–66. *Oxydoras brevis.*

Fig. 64. Ventral view of the anterior vertebræ and the "elastic-spring" mechanism; × 2.

Fig. 65. The left tripus; ventral view; × 2.

Fig. 66. Ventral view of the interior of the air-bladder; × 1½.

Fig. 67.—*Synodontis schal.* Ventral view of the anterior vertebræ and the "elastic-spring" apparatus.

Figs. 68–70.—*Callomystax gagata.*

Fig. 68. Side view of the anterior vertebræ, showing the left osseous capsule and its air-sac, the lateral cutaneous area of that side having been removed; × 2.

Fig. 69. Lateral view of the anterior portion of the trunk.

PLATE XVII.

Fig. 70. Ventral view of the osseous capsules and their contained air-sacs; × 2.

Figs. 71, 72.—*Malapterurus electricus.*

Fig. 71. Interior of the air-bladder; ventral view.

Fig. 72. Side view of the hinder part of the skull and the anterior vertebræ, showing the left elastic-spring and its protractor muscle.

Figs. 73–77. *Aspredo cotylophorus.*

Fig. 73. Base of the skull and the anterior vertebræ; ventral view.

Fig. 74. Vertical longitudinal section of the hinder part of the skull and the anterior vertebræ; × 2.

Fig. 75. Lateral view of the hinder part of the skull, the pectoral girdle, and the first, the complex, and the fifth vertebræ; × 2.

Fig. 76. Ventral view of the two air-sacs *in situ.*

Fig. 77. Ventral view of the interior of the two air-sacs.

Figs. 78–81.—*Clarias Nieuhofii.*

Fig. 78. The base of the skull, the anterior vertebræ, and the two osseous capsules; × 2:

Fig. 79. Vertical longitudinal section of the hinder part of the skull and the anterior vertebræ; × 2.

PLATE XVIII.

Fig. 80. Ventral view of the two air-sacs *in situ.*

Fig. 81. Ventral view of the interior of the right air-sac, showing the fibres of the dorsal wall and their relations to the tripodes; × 2.

Figs. 82, 83.—*Plotosus canius.*

Fig. 82. Ventral view of the anterior vertebræ and the tripodes; × 1½.

Fig. 83. Interior of the air-bladder; ventral view; × 2.

Fig. 83A.—*Saccobranchus fossilis.* Ventral view of tripus; × 1½.

Fig. 84.—*Silurus glanis.* Interior of the air-bladder; ventral view; × 1½.

Fig. 85.—*Eutropiichthys vacha.* The base of the skull, the bony capsules, and the anterior vertebræ; × 2.

Fig. 86.—*Cryptopterus hexapterus.* Ventral view of the anterior vertebræ and their processes; × 2.

PLATE XIX.

Figs. 87, 88.—*Ailia bengalensis.*

Fig. 87. The base of the skull and the osseous recesses for the tubiform air-bladder; ventral view; × 3.

Fig. 88. Lateral view; × 3.

Fig. 89.—*Schilbichthys garua.* Ventral view of the base of the skull, the right osseous capsule, and the interior of the left half of the air-bladder; × 2.

Figs. 90, 93, 94.- *Pangasius djambal.*

Fig. 90. Ventral view of the left halves of the anterior vertebræ, and the left "elastic-spring."

Fig. 93. Interior of the air-bladder; ventral view.

Fig. 94. The right tripus; ventral view.

Figs. 91, 92.—*Pangasius Buchanani.*

Fig. 91. Interior of the air-bladder; ventral view.

Fig. 92. Ventral view of the anterior chamber; × 3.

Fig. 95. *Pangasius juaro.*—Ventral view of the anterior vertebræ, and the "elastic-spring" apparatus; × 4.

Fig. 96. *Pangasius micronema.*—Ventral view of the anterior vertebræ and their

processes, showing the absence of an "elastic-spring" mechanism; the left clavicle is withdrawn from its socket; × 2.

Figs. 97, 98.—*Silondia gangetica.*

Fig. 97. Ventral view of the cavity of the air-bladder.

Fig. 98. Enlarged view of the right half; × 3.

X.—REFERENCE LETTERS.

(The lettering is uniform throughout.)

I. *Vertebral Column.*

ac.p.	Accessory articular processes.
a.c.	Aortic canal.
a.g.	Aortic groove.
c.c.	Complex centrum.
cd.c.	Cardinal canal.
c.g.	Cardinal groove.
d.l.	Dorsal lamina.
i.s.^{1}, *i.s.*^{2}.	First and second interspinous bones.
it.c.	Intercalated cartilage.
n.s.^{3}, *n.s.*^{4}.	Neural spines of the third and fourth vertebræ.
n.f.	Nutrient foramina.
o.r.	Oblique lateral ridge of the complex centrum.
pt.f.	Post-temporal facet on the transverse process of the fourth vertebra.
r.^{1}.	First rib.
r.n.	Radial nodule.
s.os.	Superficial ossification of the complex centrum.
sp.n.^{1}, *sp.n.*^{2}, *&c.*	Foramina for the exit of the first and succeeding spinal nerves.
s.v.p.	Sub-vertebral process.
t.p.^{4}.	Transverse process of the fourth vertebra.
t.p.^{4}*a.*	Anterior division of the transverse process of the fourth vertebra.
t.p.^{4}*p.*	Posterior division of the transverse process of the fourth vertebra.
t.p.^{5}, *t.p.*^{6}	Transverse processes of the fifth and sixth vertebræ.
v ^{1}, *v.*^{5}, *v.*^{6}	First, fifth, and sixth vertebral centra.
v.p.	Ventral process.

II.—*The Skull.*

al.s.	Alisphenoid.
at.a.	External atrial aperture.
b.o.	Basioccipital.

cr.c.	Cranial cavity.
c.s.i.	Cavum sinus imparis.
e.o.	Exoccipital.
e.o.^{1}.	Neural plate of exoccipital.
e.o.^{2}.	Posterior plate of exoccipital.
e.o.^{3}.	Opisthotic plate of exoccipital.
e.o.^{4}.	Horizontal plate of exoccipital.
ep.o.	Epiotic.
f.mg.	Foramen magnum.
f.s.	Cranial recesses for the sacculi (fovæ sacculi).
h.c.	Canal for horizontal semicircular canal.
l.g.	Lateral groove for the ductus sacculo-utricularis.
o.s.	Orbitosphenoid.
p.	Parasphenoid.
pt.o.	Pterotic.
pr.o.	Prootic.
s.o.	Supraoccipital.
so'.	Supraoccipital spine.
sp.o.	Sphenotic.
t.g.	Transverse groove for the ductus endolymphaticus.
tp.f.	Temporal fossa.
ut.r.	Recess for the utriculus and semicircular canals.
V, V^l.	Foramina for the Fifth cranial nerve (Trigeminal) and for its lateral branch.
VII, IX, X.	Foramina for the Seventh (Facial), Ninth (Glossopharyngeal), and Tenth (Vagus) nerves respectively.

III.—*Pectoral Girdle.*

cl.	Clavicle.
cl.s.	Socket for the head of the clavicle.
cl.p.	Posterior process of the clavicle.
cl.p'.	Additional posterior process of clavicle.
co.	Coracoid.
pt.	Post-temporal.
pt.a.	Ascending process of the post-temporal.
pt.i.	Inferior process or limb of post-temporal.
pt.p.	Post-temporal plate.
pt.s.	Descending process or stem of post-temporal.

IV.—*The Auditory Organ.*

at.	Atrial cavity.
at.a.	External atrial aperture.
a.v.c.	Anterior semi-circular canal.
c.s.i.	Cavum sinus imparis.
d.e.	Ductus endolymphaticus.
d.s.u.	Ductus sacculo-utricularis.
f.s.	Foveæ sacculi.
h.c.	Horizontal semi-circular canal.
p.v.c.	Posterior semi-circular canal.
s.e.	Sinus endolymphaticus.
s.	Sacculus.
ut.	Utriculus.

V.—*The Air-bladder.*

a.b.	Air-bladder.
a.c.	Anterior chamber.
al.c.	Antero-lateral cæcum.
a.p.	Anterior pillars.
a.s.	Air sac.
c.dv.	Cæcal diverticulum.
cp.m.	Compressor muscle.
d.p.	Ductus pneumaticus.
in.l.	Inner lateral cæcum of air-bladder.
in.st.	Inner stratum of tunica externa.
l.c.	Lateral chamber.
l.s.	Longitudinal septum.
o.l.	Outer lateral cæcum of air-bladder.
o.st.	Outer stratum of tunica externa.
p.	Peritoneum.
p.c.	Posterior cæcum.
p.p.	Posterior pillars.
pt.m.	Protractor muscle of the "elastic-spring" mechanism.
r.f.	Radial fibres of the tripodes.
r.s.	Fibrous ridge on the inner surface of the ventral wall of the anterior chamber.
sv.k.	Subvertebral keel.
sv.k'.	Projection of subvertebral keel into the dorsal wall of the anterior chamber.
t.m.	Transverse membrane.

t.s.	Primary transverse septum.
t.s′.	Secondary transverse septum.
t.t.	Tensor tripodis muscle.

VI.—*Weberian ossicles.*

c.	Claustrum.
i.lg.	Interossicular ligament.
in.	Intercalarium.
in.a.	Ascending process of the intercalarium.
in.h.	Horizontal process of the intercalarium.
sc.	Scaphium.
sc.a.	Ascending process of the scaphium.
sc.s.	Spatulate process of the scaphium.
s.pv.	Saccus paravertebralis.
tr.	Tripus.
tr.a.	Anterior process of the tripus.
tr.ar.	Articular process of the tripus.
tr.c.	Crescentic process of the tripus.
tr.h.	Heel-like process of the tripus.
v.r.	Ventral ridge of the tripus.

VII.—*Other structures.*

ac.br.	Accessory branchiæ.
ap.m.	Aponeurotic membrane.
d.l.m.	Dorso-lateral muscles of the trunk.
l.c.a.	Lateral cutaneous areas.
lgt.	Ligament.
l.l.c.	Lateral line canal.
mes.	Mesentery.
mph.	Mesonephros.
mph.r.	Recesses for the "head" kidney.
œs.	Œsophagus.
p.c.s.	Peritoneal cul-de-sacs for the lateral lobes of the liver.
v.l.m.	Ventro-lateral muscles of the trunk.

Bridge & Haddon.

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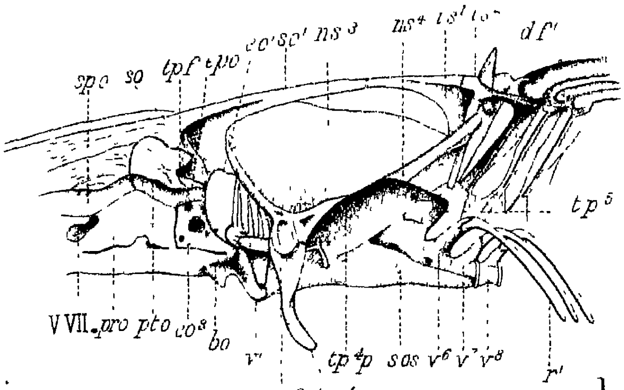

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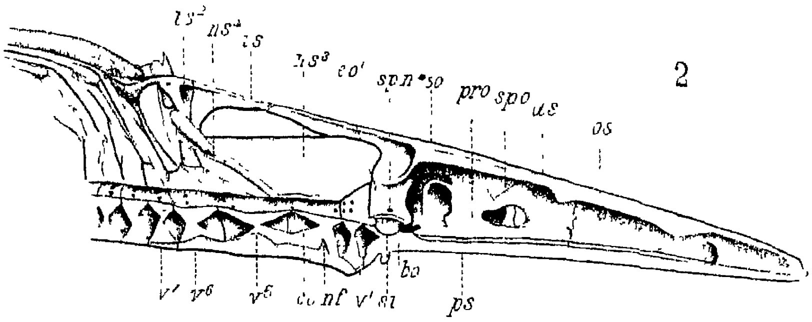

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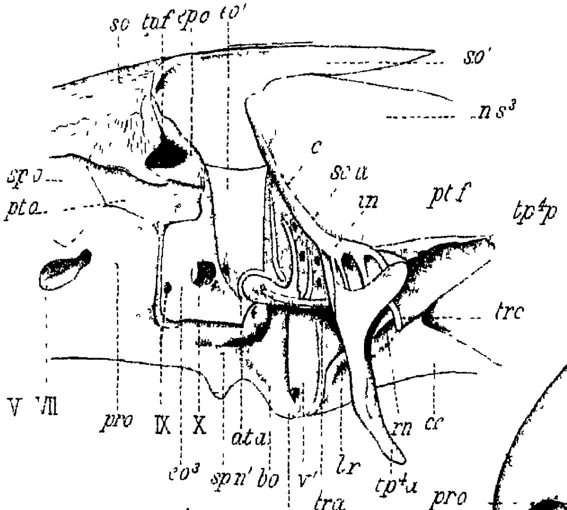

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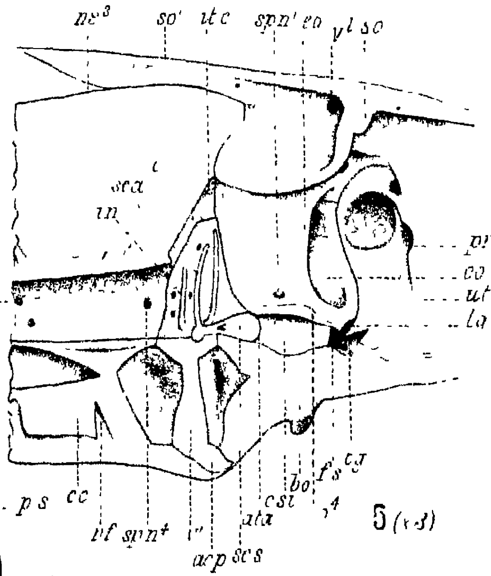

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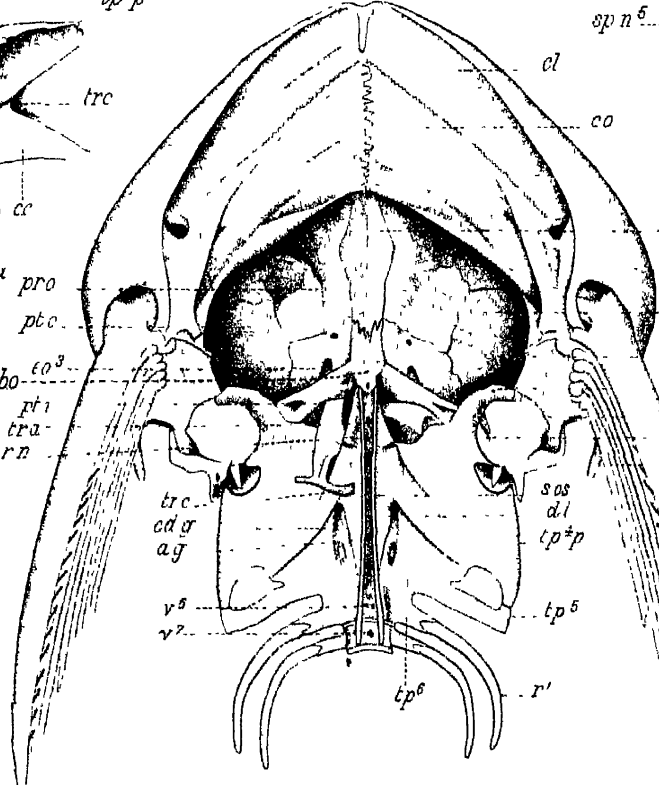

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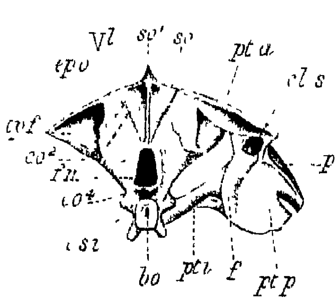

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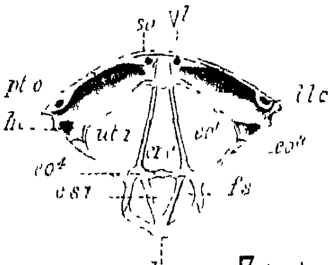

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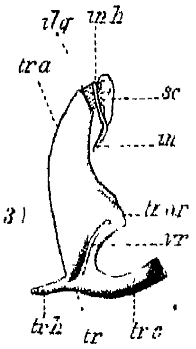

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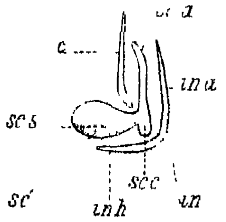

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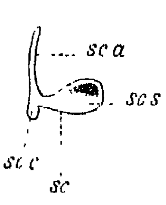

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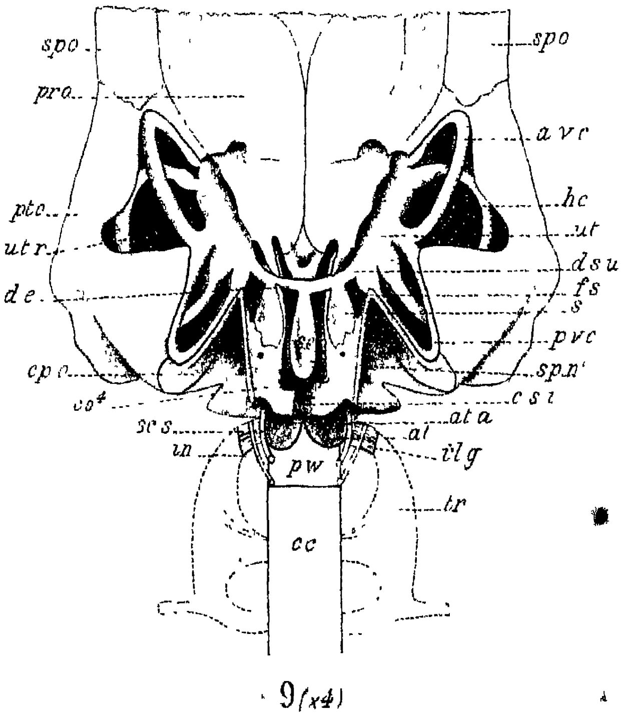

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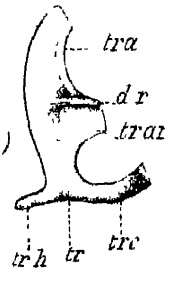

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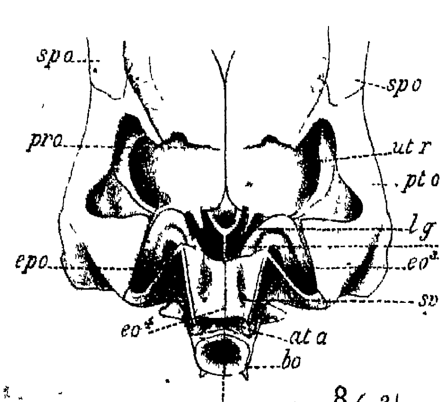

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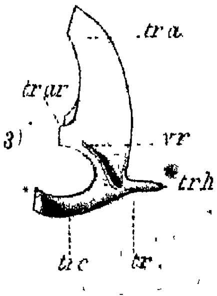

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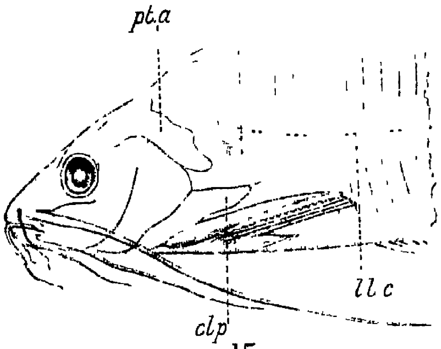

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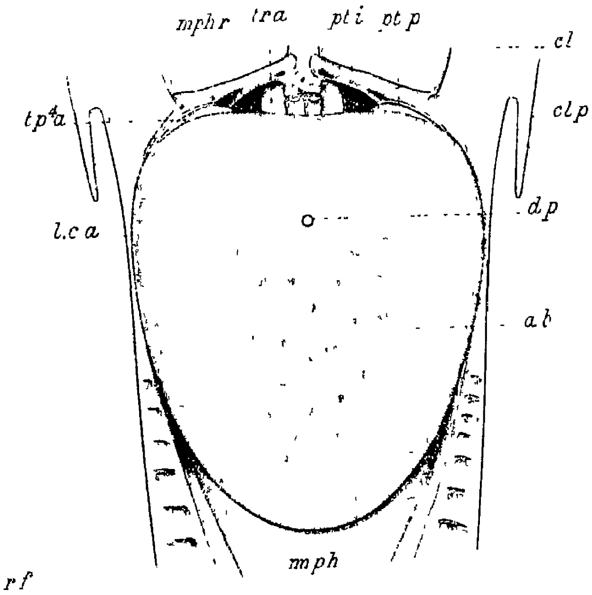

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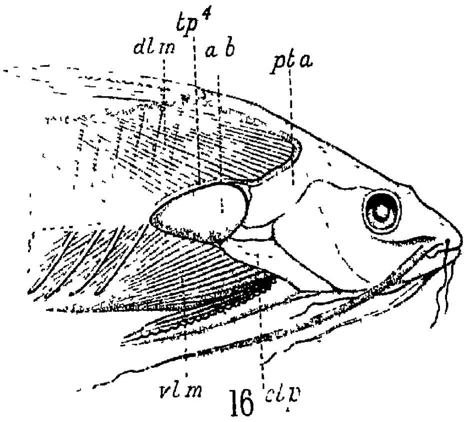

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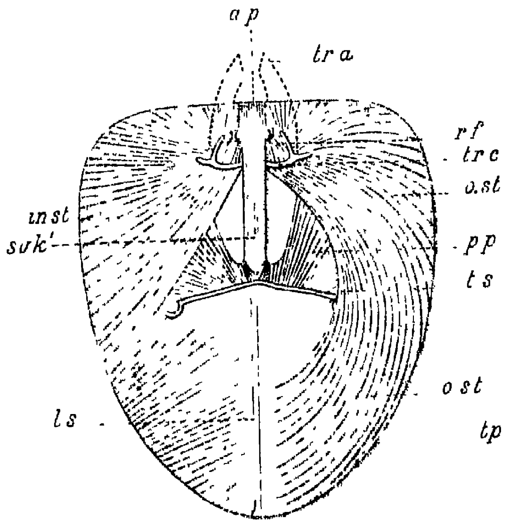

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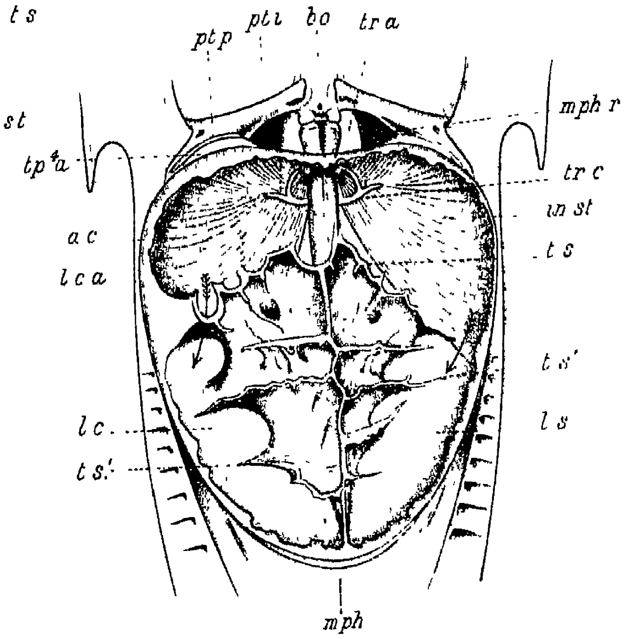

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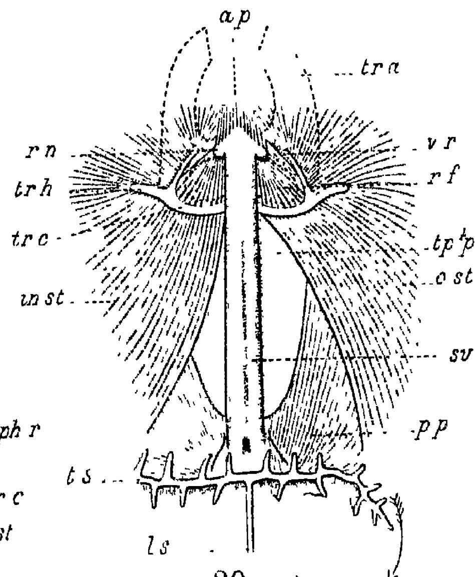

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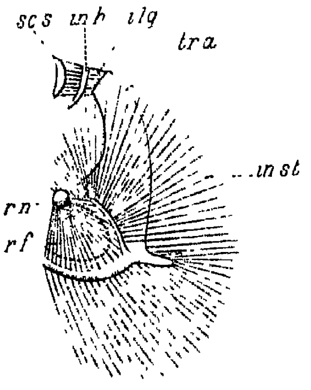

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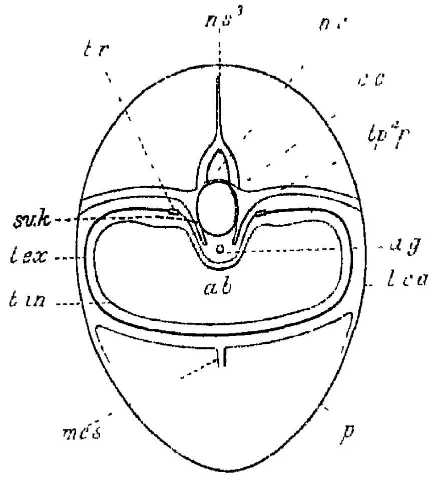

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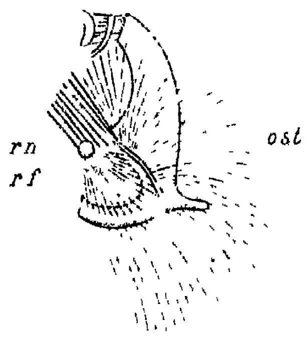

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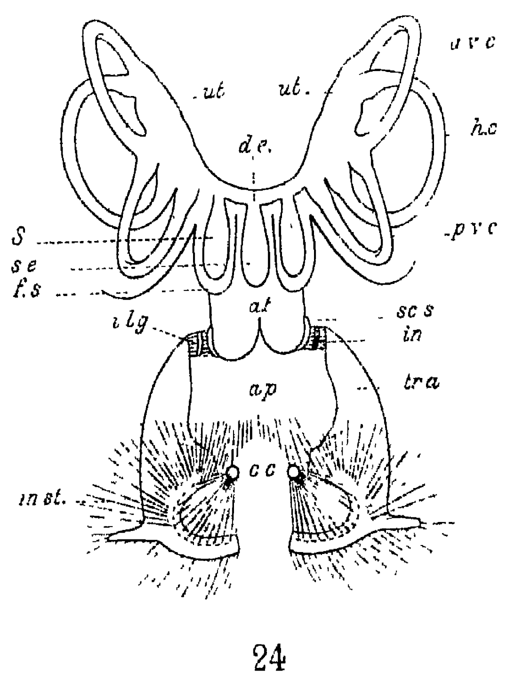

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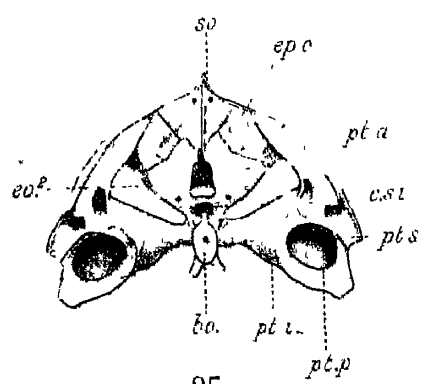

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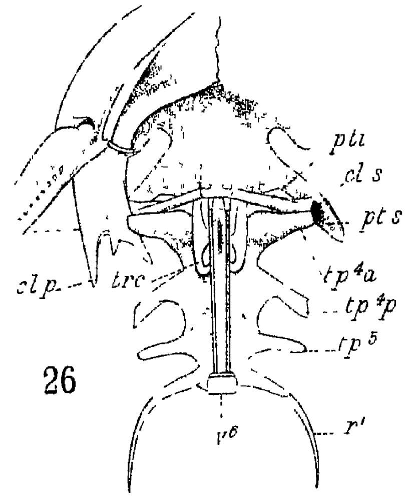

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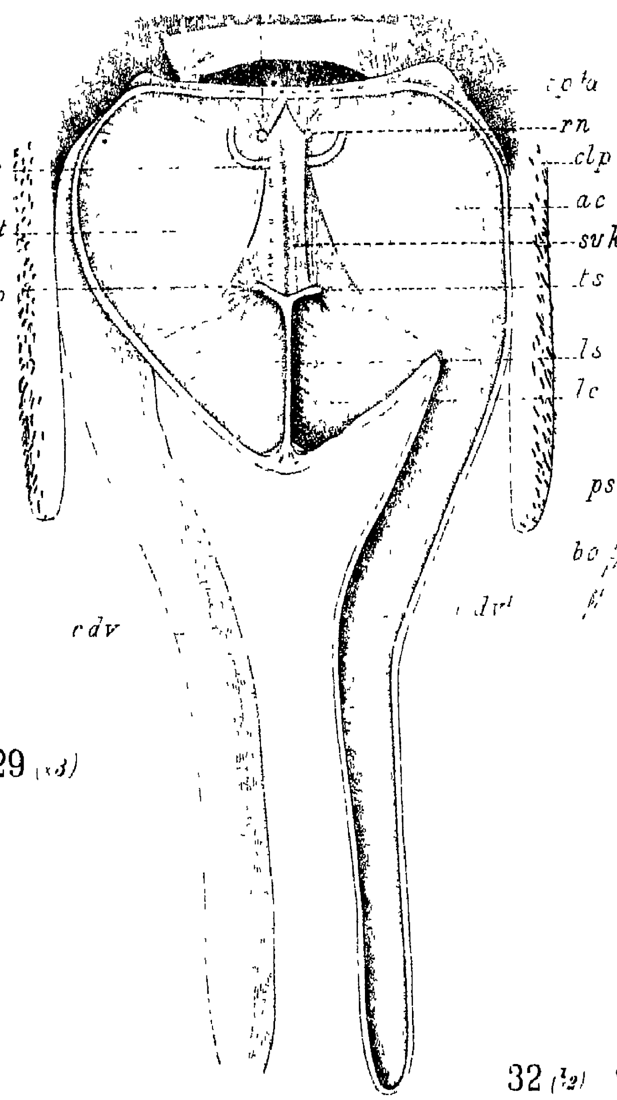

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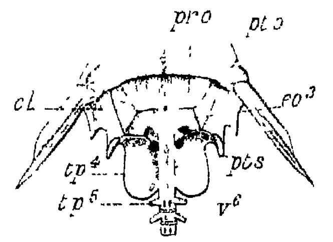

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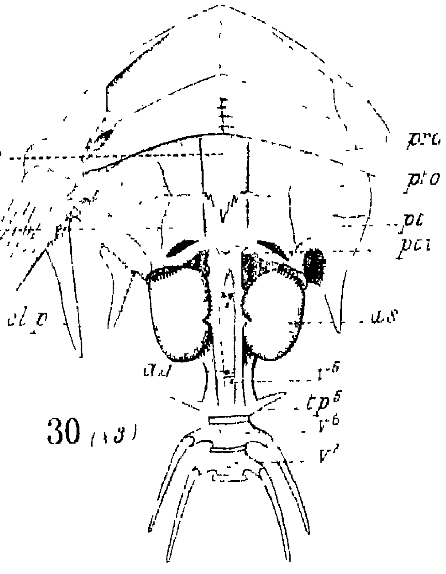

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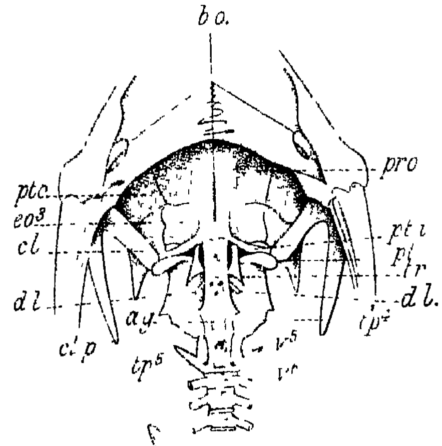

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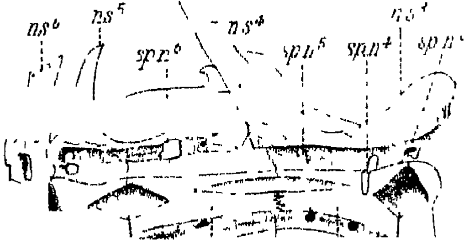

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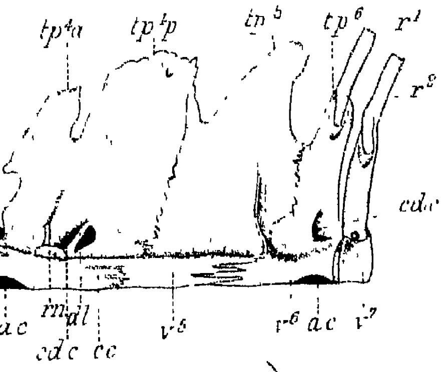

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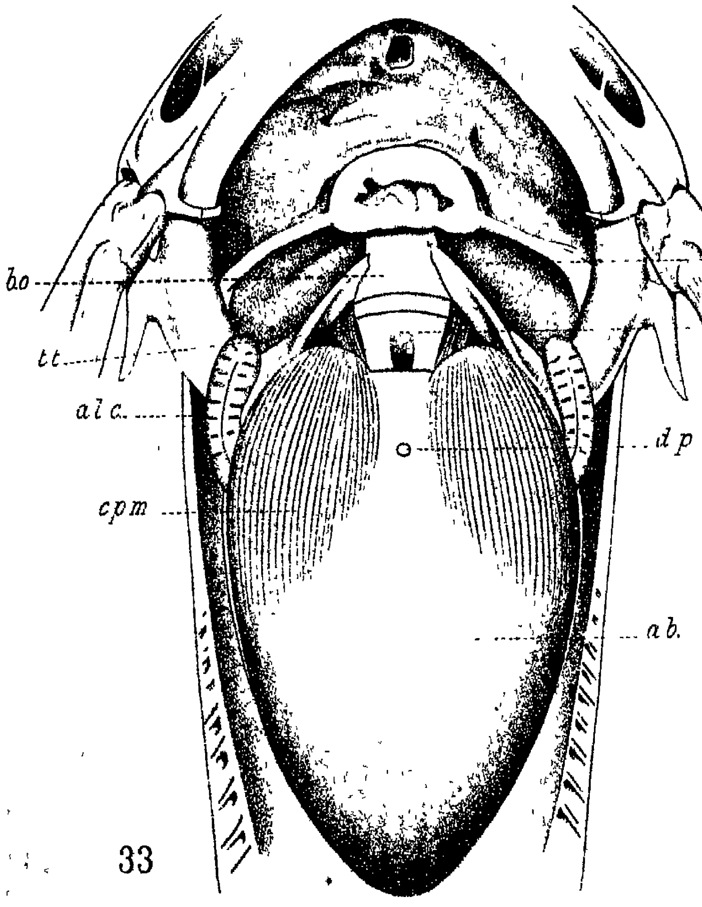

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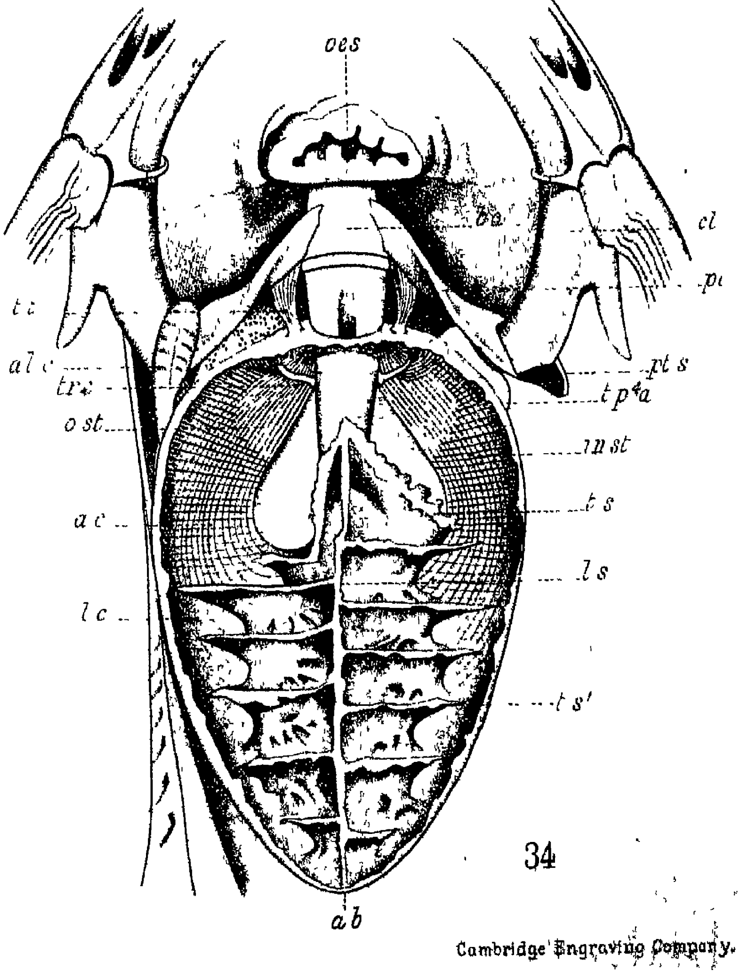

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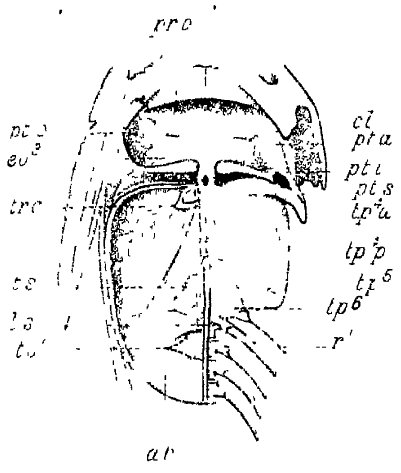

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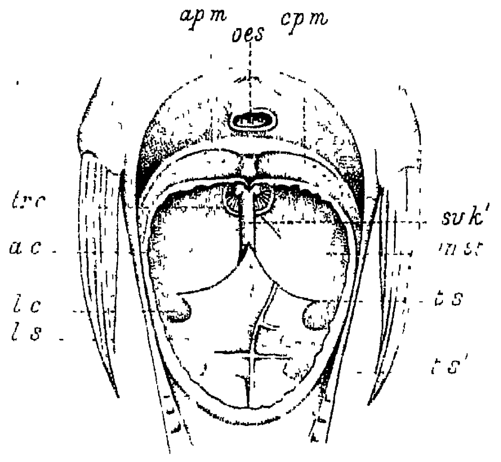

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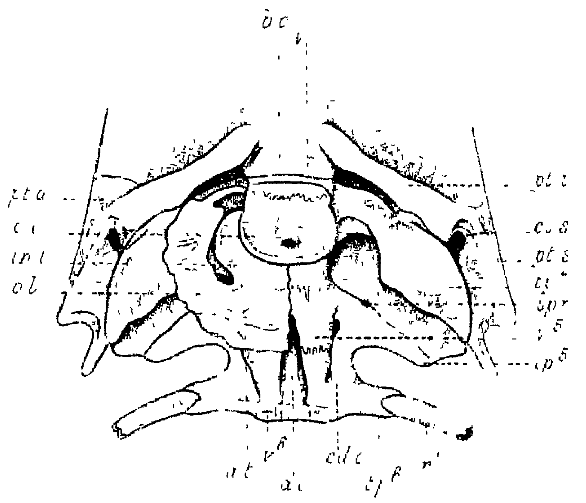

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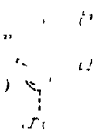

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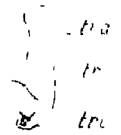

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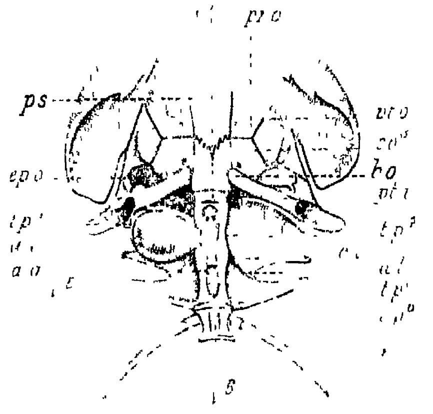

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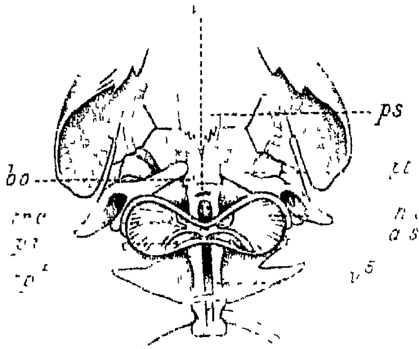

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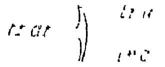

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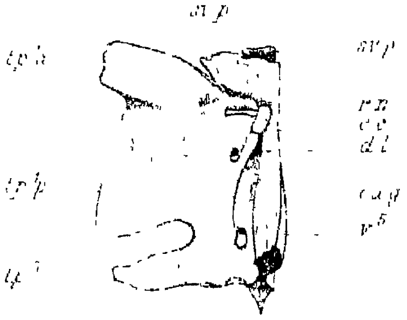

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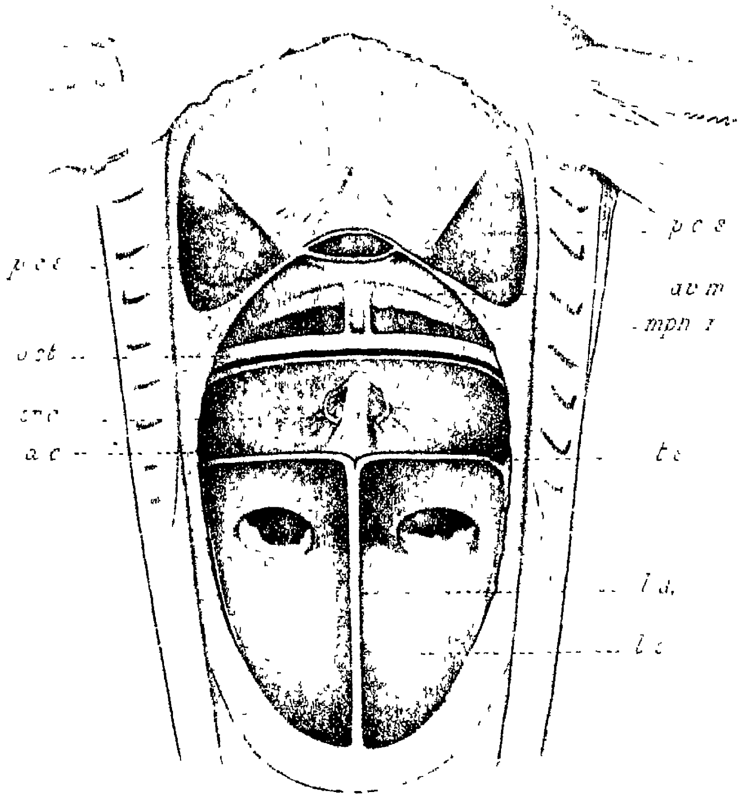

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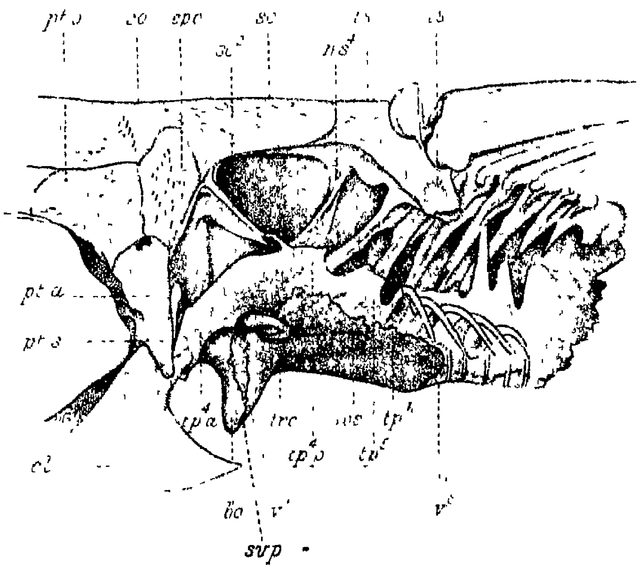

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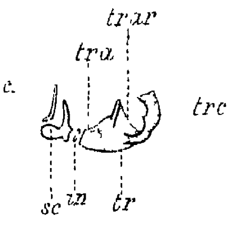

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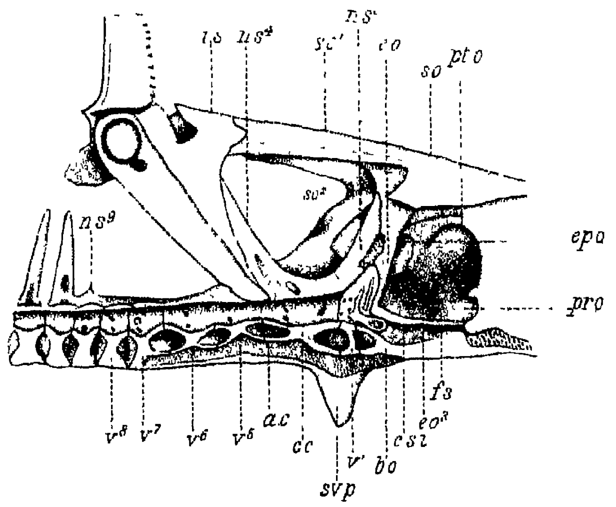

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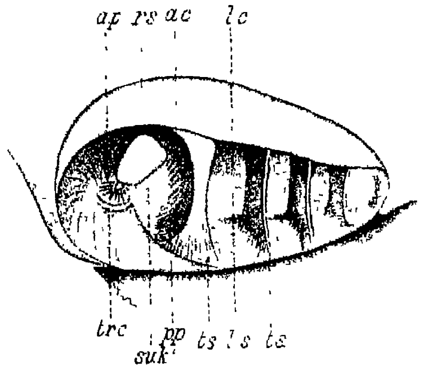

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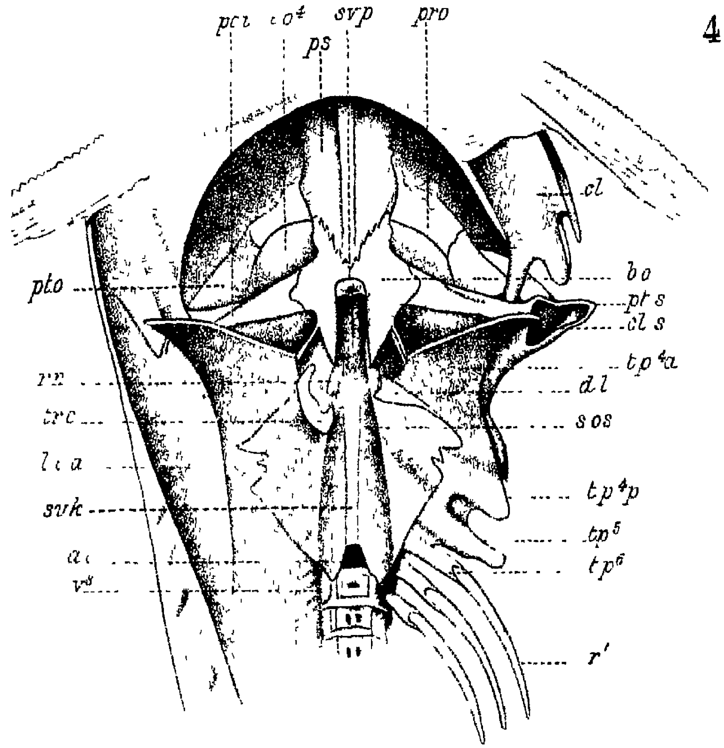

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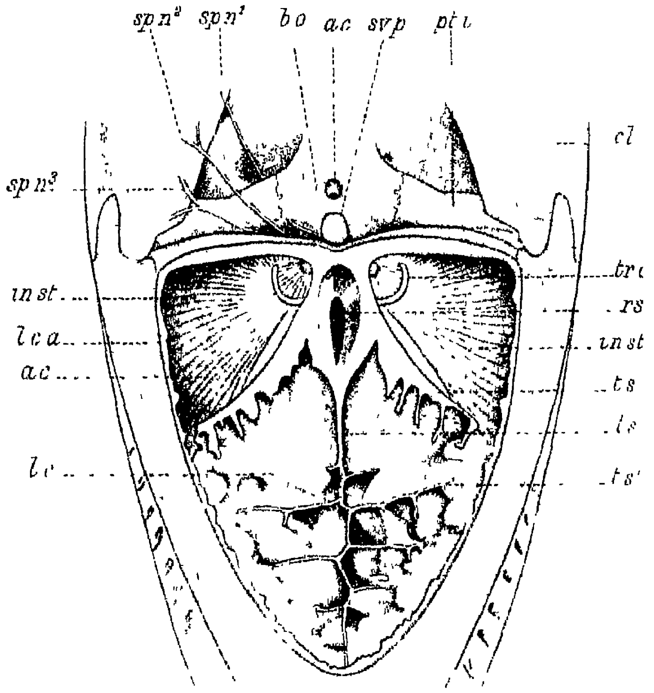

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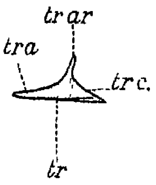

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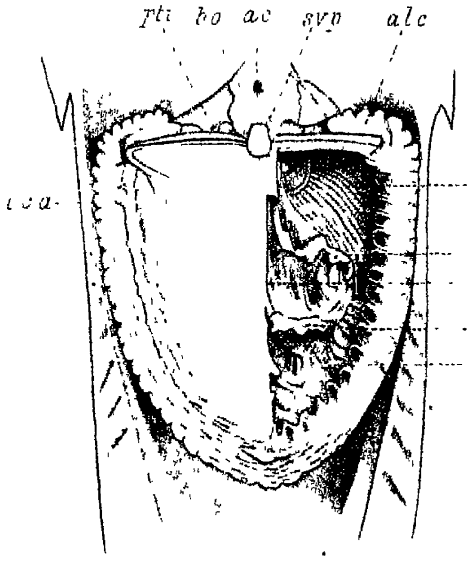

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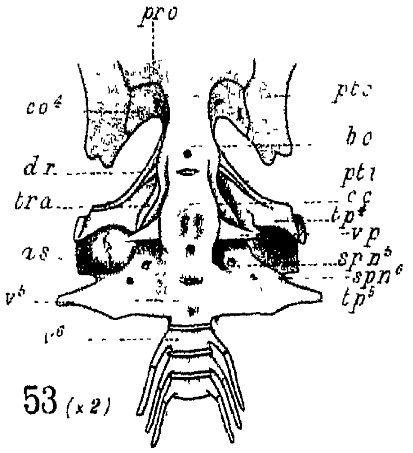

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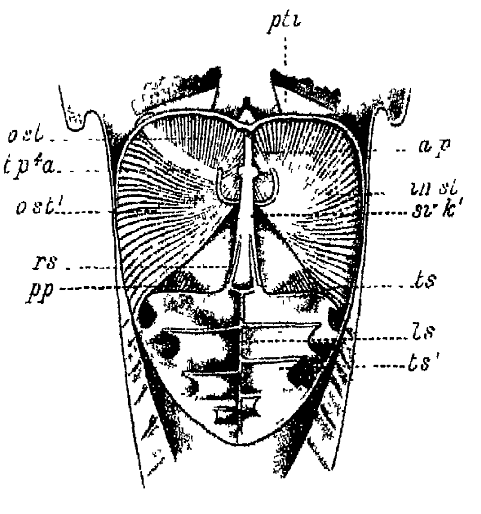

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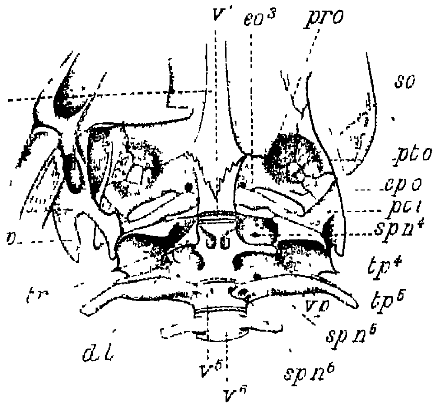

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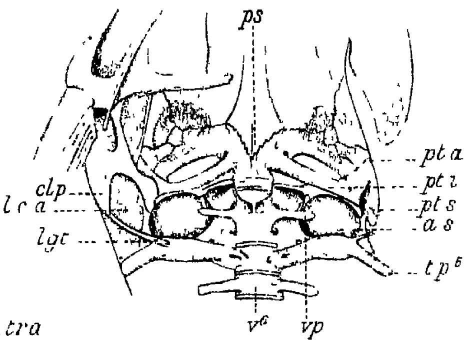

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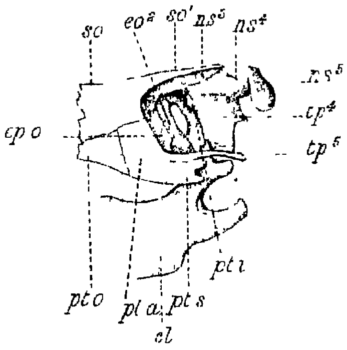

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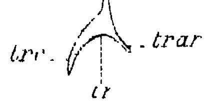

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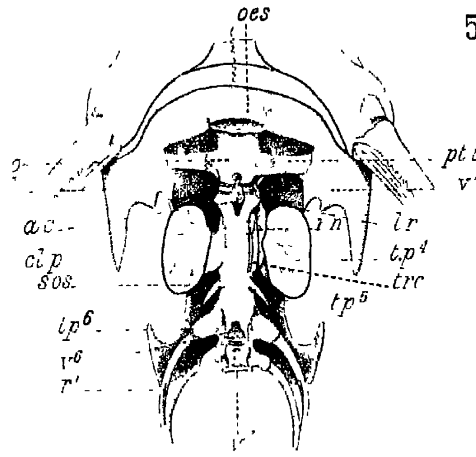

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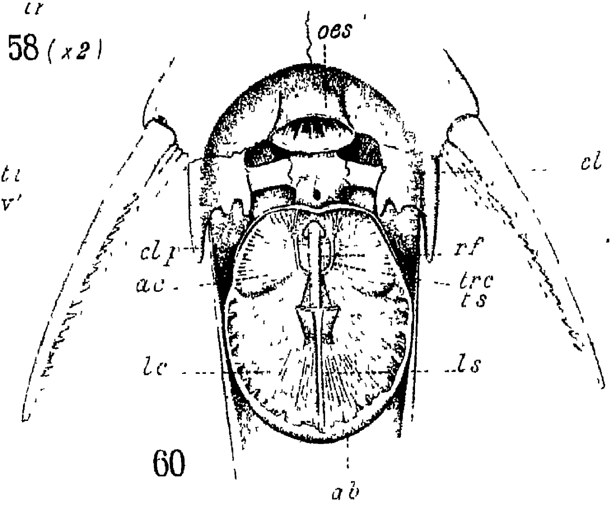

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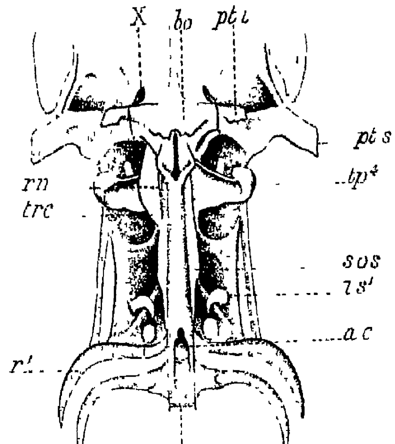

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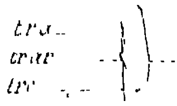

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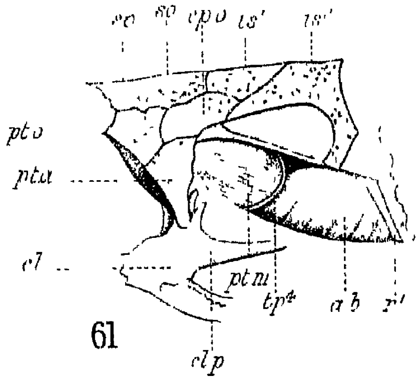

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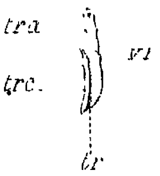

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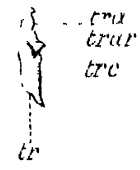

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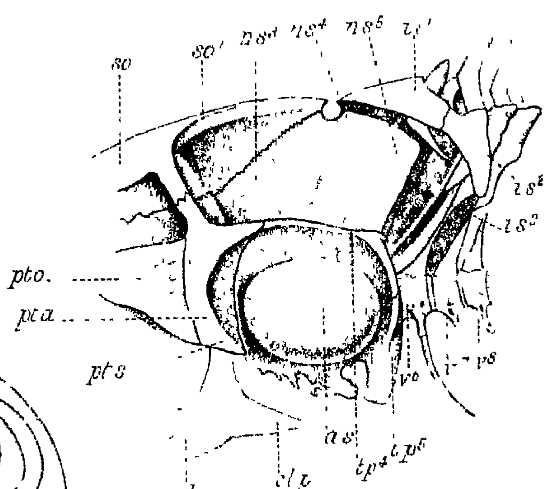

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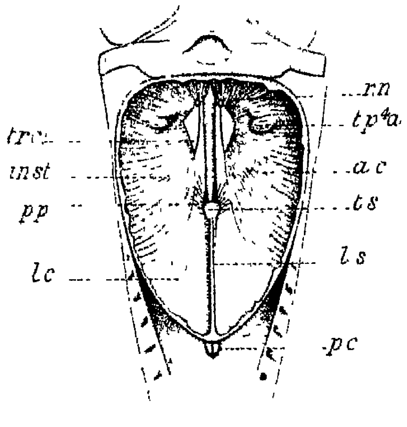

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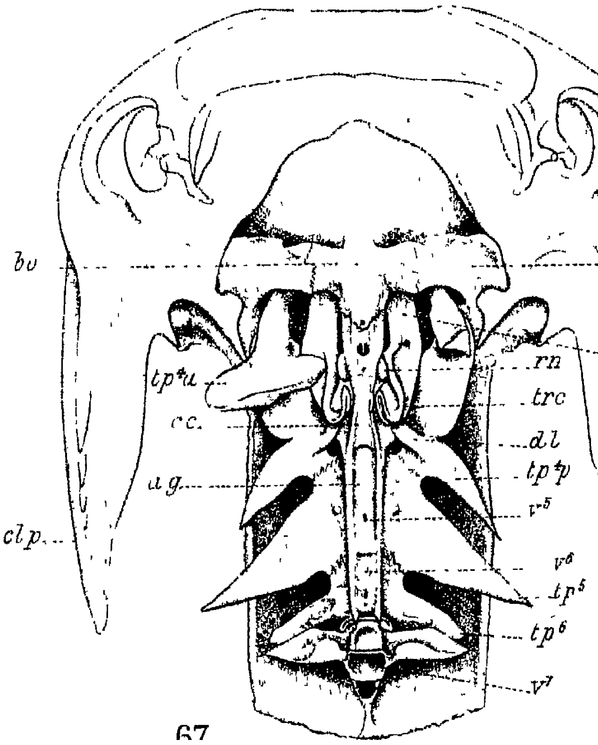

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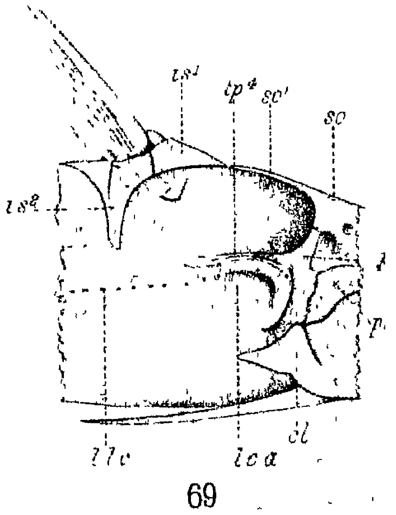

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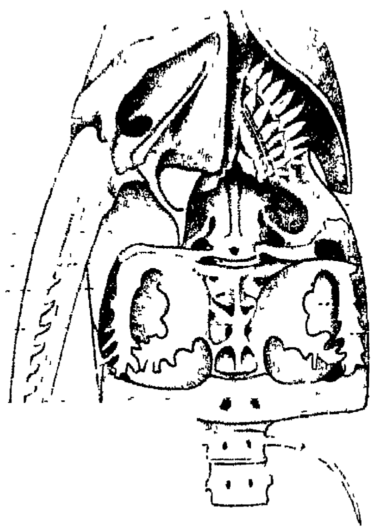

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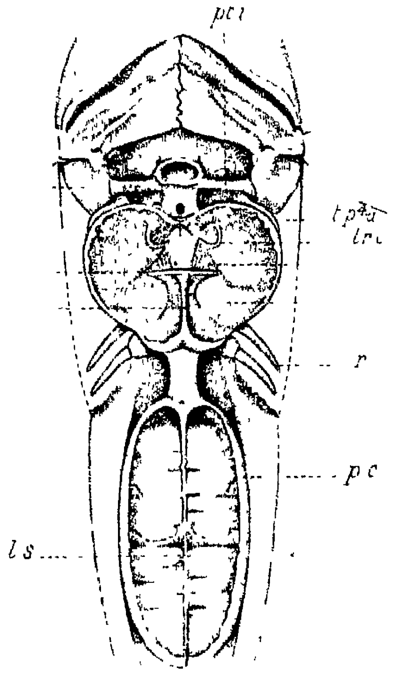

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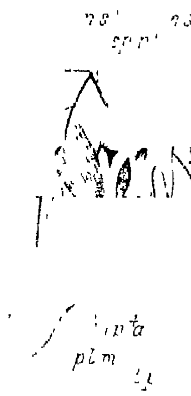

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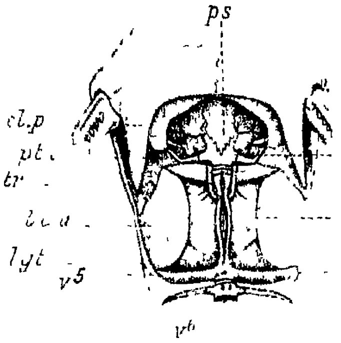

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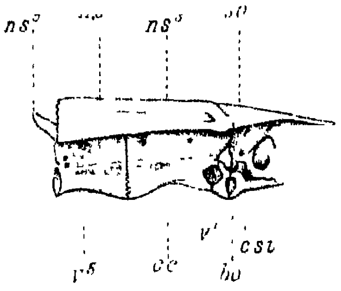

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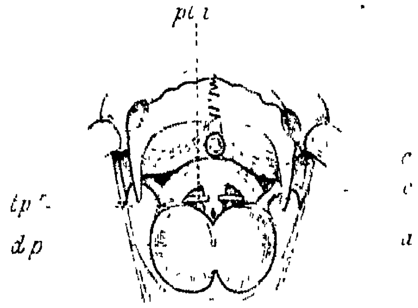

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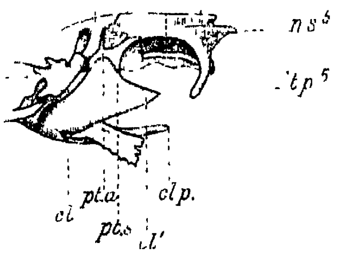

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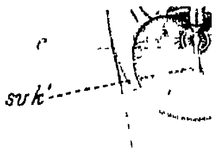

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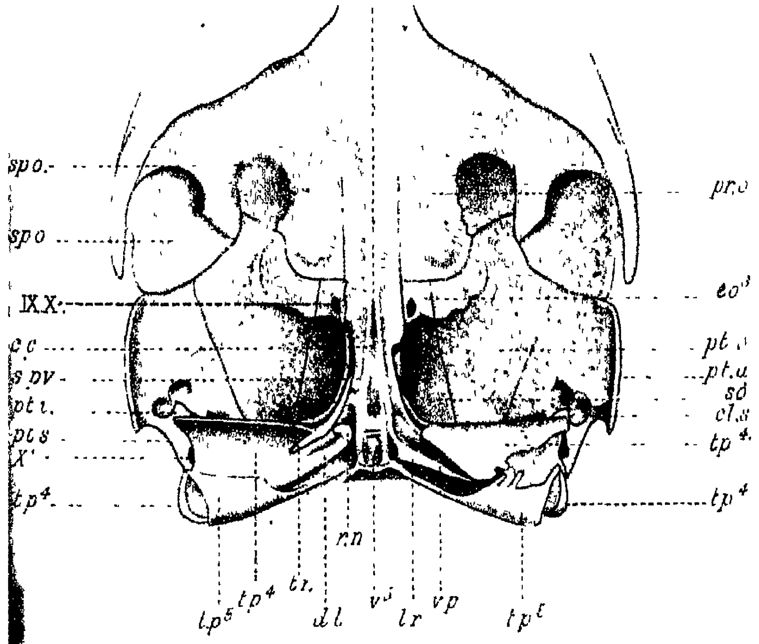

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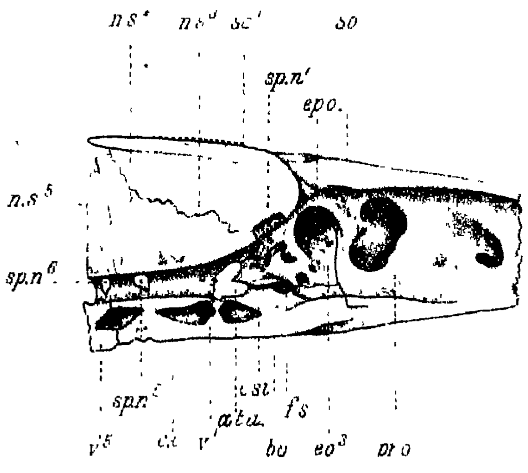

79 (×2)

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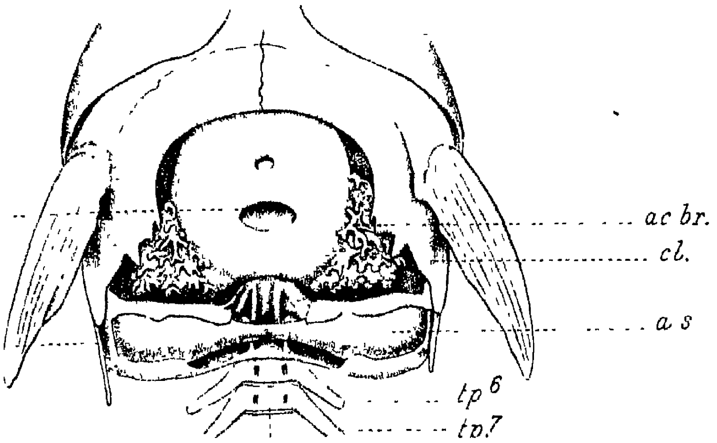

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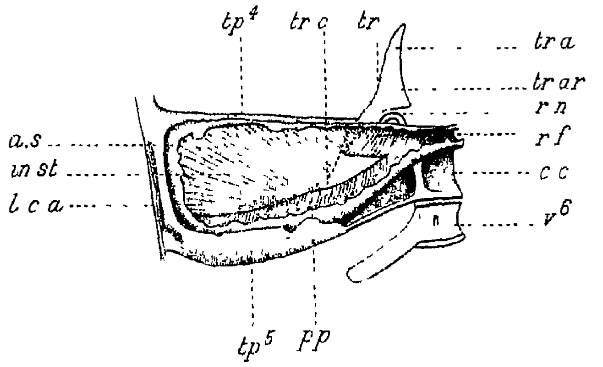

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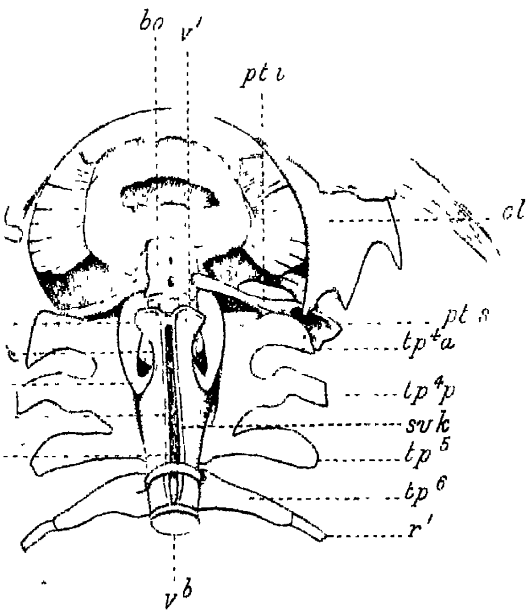

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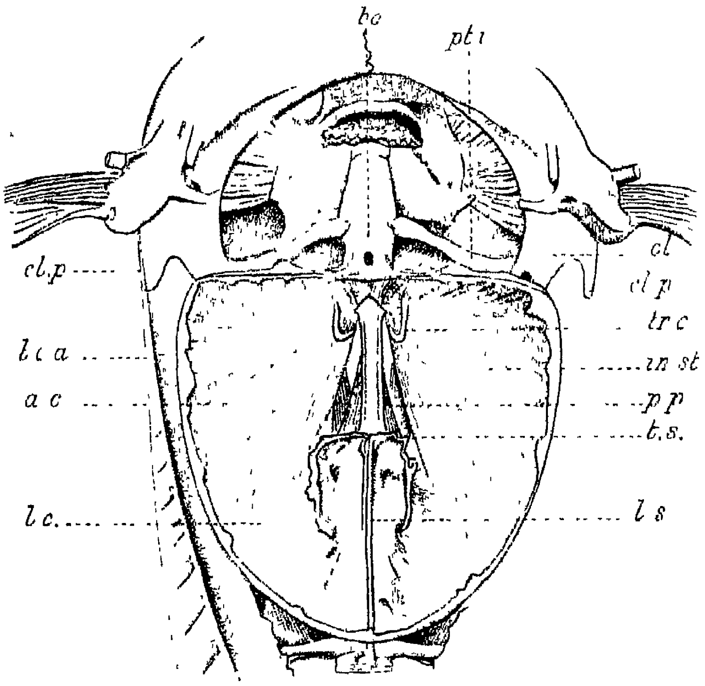

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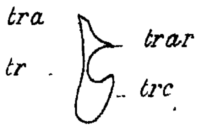
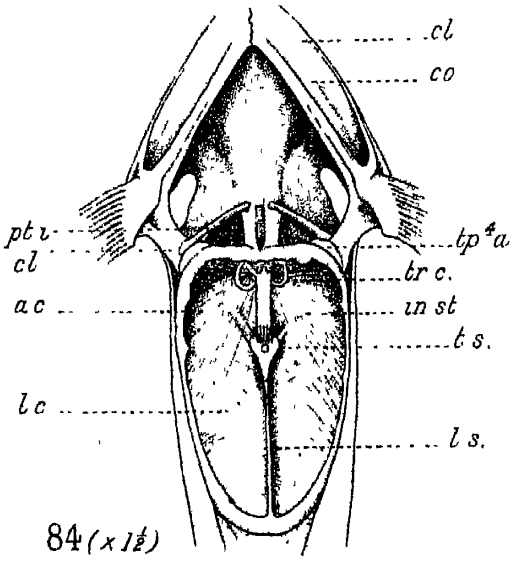


83a. (×1½)



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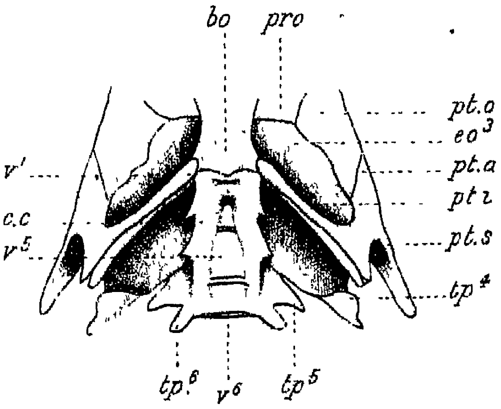

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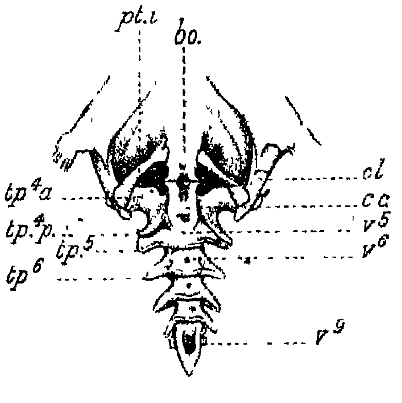

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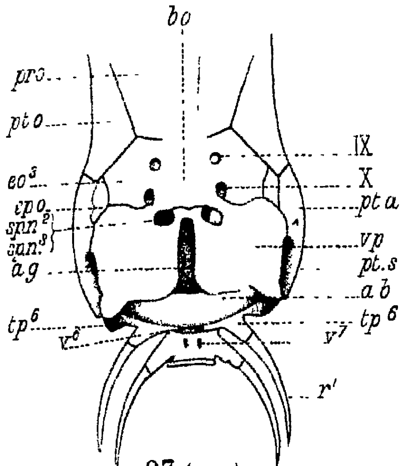

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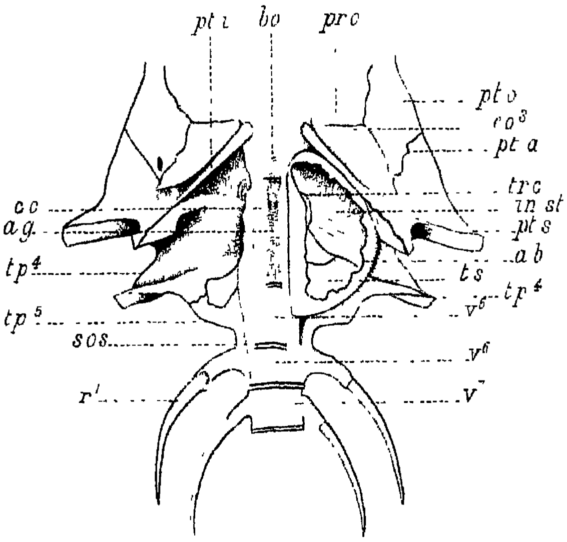

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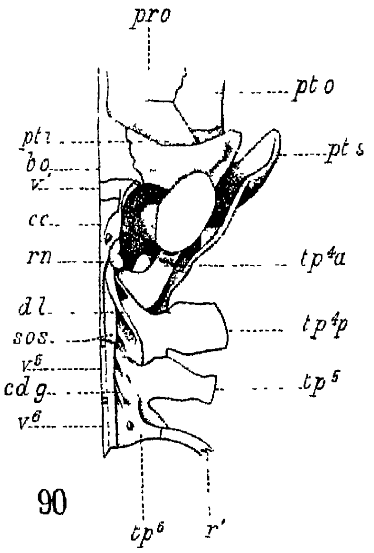

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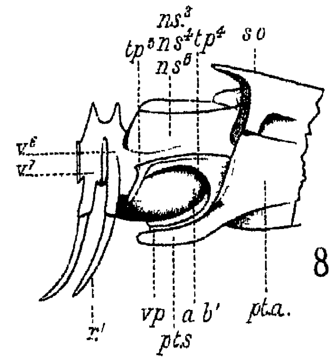

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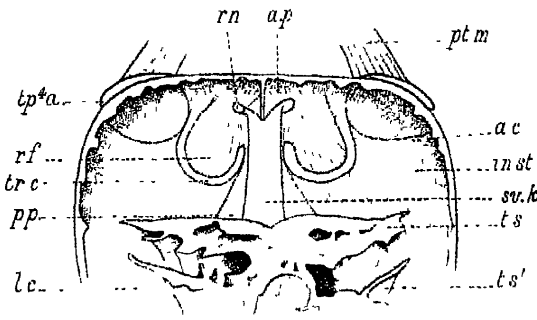

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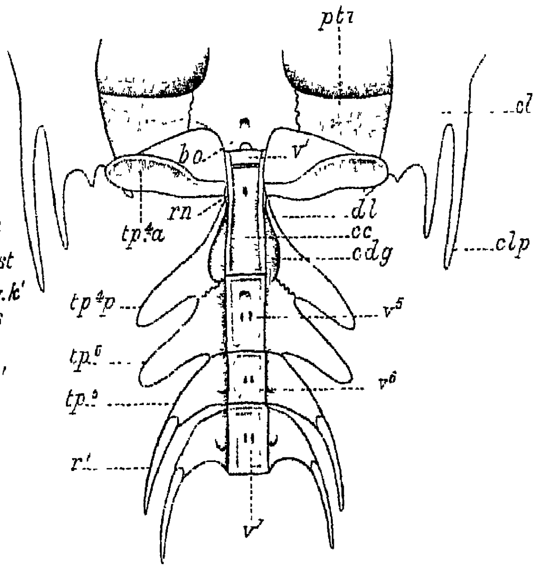

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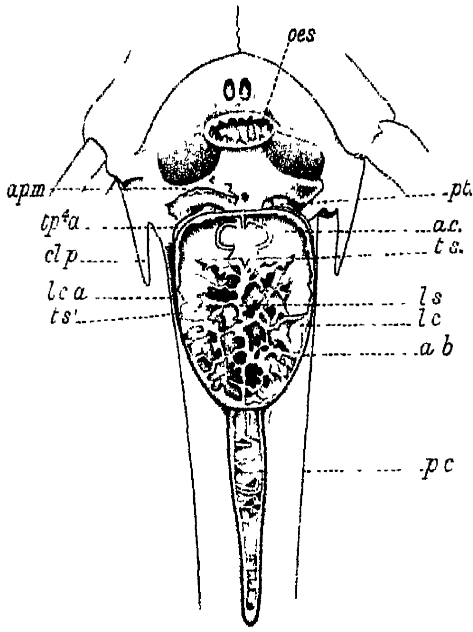

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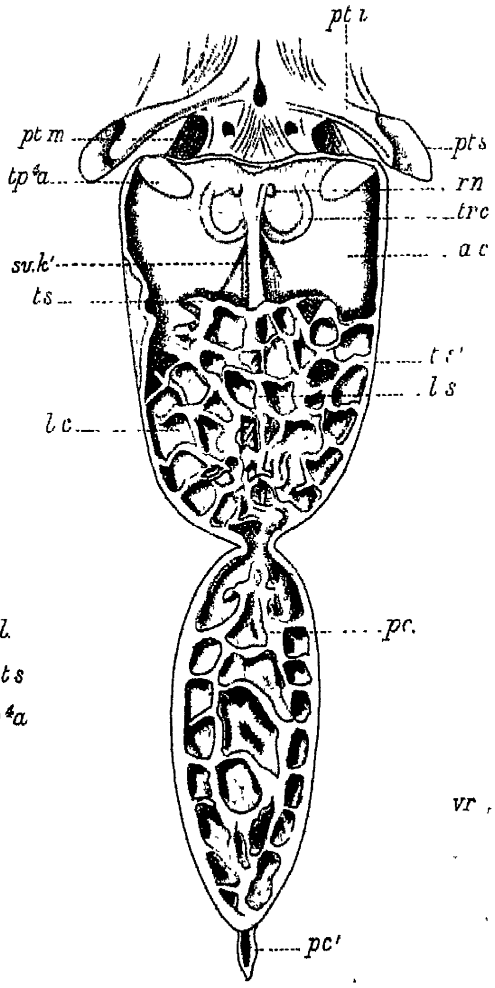

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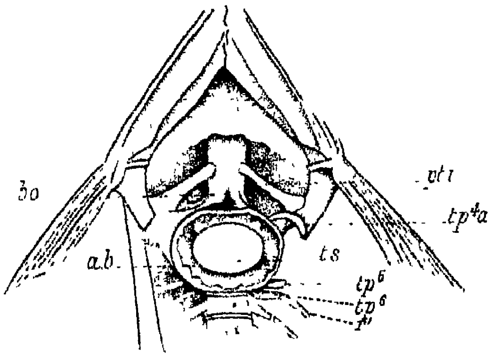

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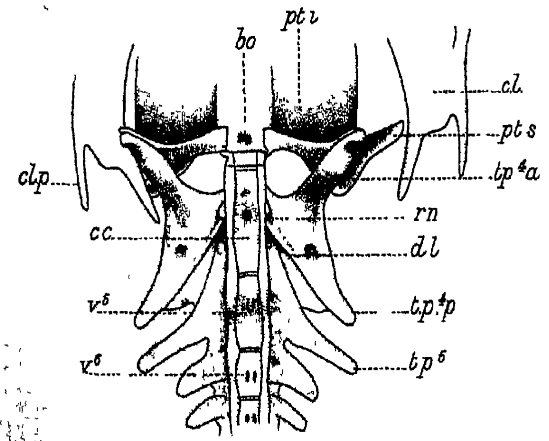

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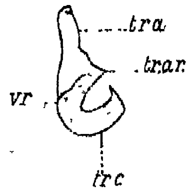

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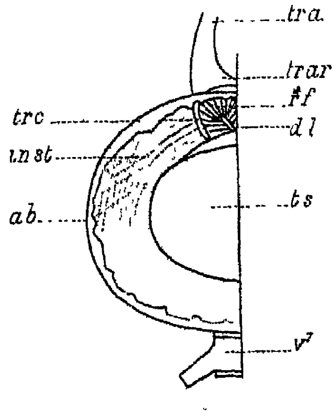

98 (×3)

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IV. *The Electromotive Properties of the Skin of the Common Eel.*

By E. WAYMOUTH REID, *Professor of Physiology in University College, Dundee, St. Andrew's University, N.B.*

Communicated by Professor M. FOSTER, *Sec.R.S.*

Received November 19,—Read December 15, 1892.

HERMANN (1) has investigated the electromotive properties of the skins of Fish. His object in so doing was to attempt to determine, by the employment for experiment of a skin usually credited with being bereft of glands, whether the marked "current of rest" exhibited by the skins of Amphibia is with greater probability to be ascribed to glandular processes in accordance with the opinion of DU BOIS REYMOND (2), or whether the phenomena are not explained with greater simplicity upon the principles of his own 'Alterations-Theorie.' DU BOIS failed to obtain evidence of a "current of rest" in the four kinds of Fish with which he worked (Eel, Tench, Pike, and Perch), a fact, which taken in conjunction with the absence of "glands," satisfied him that in the richly glandular Amphibian skin the source of the E.M.F. must lie in the secreting structures. HERMANN himself, previous to his examination of the skins of Fish, shared to some extent the opinion of DU BOIS, for in a paper published in 1878 (3), he inclines to the idea, that preparatory processes of glandular origin are the cause of the E.M.F. of the current of rest in the skin of the Frog, but also advances the supposition of a possible contribution from epithelial action at the surface. Finally, as is well known, HERMANN demonstrated the presence of an ingoing current of rest in the skins of some ten genera of Fish, but found that its E.M.F. was far less than that exhibited by the Amphibian skin. After noting that substances, the application of which destroys the current of rest in Amphibian skin, cannot be traced microscopically beyond the upper layers of epidermic cells, and recalling the fact that an electromotive excitatory change was demonstrated by BACH and OEHLER (4), in the skin of the Frog, after complete removal of the current of rest, by the action of corrosive sublimate applied to the outer surface, HERMANN concludes that the E.M.F. of the current of rest, and that of the current of action are of different origin. In speaking of the origin of the current of rest, he makes the following statement, upon the strength of his demonstration of such a current in the "non-glandular" skins of Fish, "dass nicht, oder nicht in erster Linie, die Drüsen, sondern die Epithelschicht, der Sitz der elektromotorischen Hautwirkung ist." Finally he bases his explanation of the source of the E.M.F. of the current of rest of the skins of both Amphibians and Fish upon the axioms of the "Alterations-Theorie." According to this hypothesis, the processes of dying or excitation in the continuity of protoplasm cause the more altered parts to be negative electrically to the less altered, so HERMANN says "Nun haben wir aber zunächst in allen verhornenden Epithelgebilden eine dem Absterben völlig analoge Alteration, welche von aussen nach innen fortschreitet (und durch den Nachwuchs compensirt wird), nämlich die Verhornung." Thus in the case of the Amphibian the keratinized superficial cells of the epidermis are supposed to form a demarcation surface whose electrical sign is negative to that of the deeper less altered portions of the skin tissue.

Analogous to the "keratin-metamorphose" of protoplasm stands in this connection a "mucin-metamorphose," and HERMANN remarks "Am Aal und an der Trüsche kann man direct sehen, wie die äusseren Zellenden unter Mucinbildung zu Grunde gehen."

A protoplasmic alteration, then, on the down-grade side of cell life is the explanation offered of the source of the E.M.F. of the current of rest of the skin of Amphibian and Fish, and the case of the latter is taken to throw light upon the former, since the complication due to the presence of glands is absent.

The explanation for the case of the Fish (mucin-metamorphose) is further supported by a reference to ROSENTHAL'S (5) discovery of an ingoing current in the mucous surface of the stomach and gut of the Frog and Rabbit, and the statement that OEHLER has demonstrated a current with similar direction in the integument of the Snail.

Is it correct to consider the skins of Fish as being non-glandular? If the term "gland" be restricted to collections of secretory cells, in the form of definite organs, such as exist in Amphibian skins, then it is certain that, with the exception of the special case of the dermal glands of Myxinoids, "glands" are absent from the skins of Fish. But if one include under the designation of "gland" any cells capable of forming a secretion—calling such cells, as is usual, "unicellular glands"—then, on the other hand, it must be admitted that the skins of Fish are richly glandular. One has but to turn to the histological works of LEYDIG (6 and 7), F. E. SCHULZE (8), FŒTTINGER (9), LIST (10), and many others, in order to be convinced that unicellular secretory organs not only exist in the skins of Fish, but are in many cases of a high degree of complexity. In the case of the common Eel, ordinary goblet cells, and also the special "kolben" first described by KÖLLIKER (11) for the skins of *Myxine* and *Petromyzon*, compose more than half the structures of the epidermis; and, by comparison of the histology of resting and stimulated skins in this Fish, I have convinced myself that both these structures are engaged in the act of secretion of slime, the goblet cells supplying a mucinous matter, and the "kolben" passing into the fine threads that occur in the slime. The details of this process of secretion must be reserved, however, for another communication. The demonstration, therefore, of a current of rest in the skins of Fishes, is not of necessity a proof of HERMANN'S explanation, seeing that active secretory processes are at work in such structures. Moreover, HERMANN'S statement that one "kann direct sehen wie die äusseren Zellenden unter Mucinbildung zu Grunde gehen" is not substantiated by microscopic examination of the skin of the Eel. In the metachromatic staining reaction of thionin, as worked out by HOYER (12) one has, I am convinced, a reliable microscopic test for the presence of mucin. If sections of Eel-skin, treated with corrosive sublimate, be stained with this substance, it is the goblet cells alone—and these occur in the deep layers of the epidermis as well as near the surface—that give the characteristic reddish-violet colour, the surface epidermic cells staining bright blue. I propose in the following pages to attempt to demonstrate that the current of rest in the case of the Eel is more probably associated with active preparatory processes in its glandular elements, as HERMANN originally thought to be the case for the Frog, than with any keratinous or mucinous demarcation surface in accordance with his later writing; at the same time it will be shown that both negative and positive variations of the current of rest can be elicited by suitable experimental treatment of the removed skin of the Eel.

The Eel has been chosen for experiment principally on account of the fact that it can be flayed without the removal of any of the subjacent muscular tissue, but also because it is easily obtained with little injury, and lives well in captivity.

METHOD.

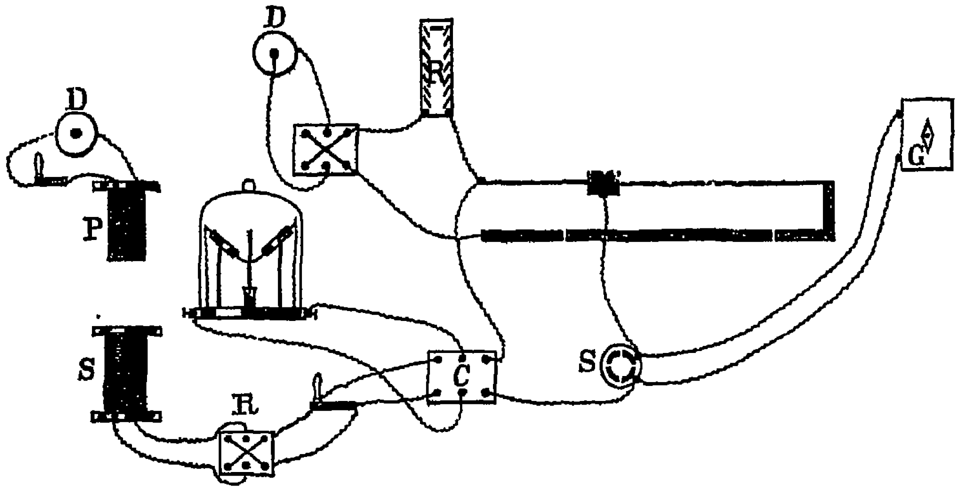
Eels, caught in the River Tay without the use of a hook, were transferred as quickly as possible to the laboratory, and kept in running water. Death was effected by transfixion of the medulla, the utmost care being taken not to injure the surface of the skin. Pieces of skin of an area of from 9 to 16 square centims. were removed from the back and sides, and were pinned by means of hedgehog bristles upon a suitable cork frame.

The supported piece of skin was fixed in the special moist chamber devised for the electrical examination of membranes by ENGELMANN (13), and led off by the ordinary non-polarisable electrodes, provided with crochet cotton contacts soaked in physiological salt solution. The galvanometer (ELLIOTT, 20,000 ohms R.) was arranged with the usual compensating circuit supplied with a Daniell cell of very low resistance.

The general plan of circuit is evident from the wood-cut, fig. 1.

By means of a paraffin switch, C, it was possible to stimulate the skin by the current of the secondary coil, S, through the electrodes, with the galvanometer circuit broken, and immediately, by turning over the key, to turn the skin current into the compensating circuit. The reverser, R′, was introduced for purposes of testing for possible polarisation of electrodes, but with the strengths of stimulating current employed this was not found to occur. The moist chamber was furthermore provided with an inlet and outlet tube, so that gases or vapours could easily be introduced and subsequently removed without any disturbance of the electrical contacts.

Fig. 1.



The Electromotive Force and Direction of the "Current of Rest."

[Hermann quotes ·003 – ·007D for the value of the E.M.F. of the current of rest of the Eel's skin, while Bayliss and Bradford (14) give ·00569 volt for one case. In the course of these experiments I have observed variations from ·00072 – 00936D. As regards the direction of the current, both Hermann and Bayliss and Bradford found it to be ingoing. Though this is the rule, and is always the final result, yet it is not uncommon to find an outgoing current indicative of inner surface negative to outer immediately after setting up the preparation. With time the direction of this abnormal current reverses to the normal. Even if the current is in the normal direction at the first, its E.M.F. generally continues to rise for some time. The conditions that favour the presence of an abnormally directed current of rest are: (i.) the examination of pieces of exsected skin immediately after a process of capture in which the skin secretory mechanism has been greatly tried; (ii.) absence of special care in removal.

As regards the source of the E.M.F. of the normally directed current of rest, it is not in difference of reaction between the two surfaces, for the inner surface is normally more alkaline to litmus than the outer, a condition that would, *per se*, lead to an outgoing current. Moreover, I cannot see that mucin-metamorphosis can be adduced, seeing that microscopic observation shows no evidence of this in the surface scales of the epidermis.

It is more probable, as will be seen in the sequel, that the source of the E.M.F. of the current of rest lies in glandular preparatory processes occurring in the secreting elements of the epidermis.

The amount of the E.M.F. of the normal current is associated with the vigour of the animal—a fact noted for the Frog by du Bois, Budge (15), and Engelmann.

As regards the explanation of the abnormally directed current of rest observed often immediately after putting up the preparation, and especially in Eels fatigued in the process of capture, it is possible that either or both of two causes may contribute to its production : (i.) injury to the inner surface during removal tending to produce an outgoing current; (ii.) depression of epidermic activity from fatigue, or "shock" of removal, causing a temporary diminution in the E.M.F. of the normal ingoing current.

Two contacts upon the outer surface will often give evidence of difference of potential, but I have never read more than ·0012D, about one-fifth of the average E.M.F. between inner and outer surface. This difference between two points on the outer surface is to be attributed to an unequal distribution of secreting elements (especially the "kolben") often observed in microscopic sections.

Mechanical stimulation in the region of one of the externally placed electrodes causes an increase of the negativity of that electrode (see p. 359), a fact much against the mucin-metamorphosis theory of origin of E.M.F.

The fact of proximity of an electrode to a gland mass favouring its negativity is demonstrable on the outer surface of the skin of the Toad, where with two thread electrodes it is found that there is greater difference of potential when one is on a "gland wart" and the other between two, than when both are over glands. Here, however, mechanical stimulation leads to diminution of negativity.

Two points on the inner surface of the skin of the Eel show no appreciable difference of potential.

I am of opinion, therefore, that it is probable that the source of the E.M.F. of the current of rest of the skin of the Eel is in the secretory activity of its unicellular glands.—March 2, 1893.]

Action of Carbonic Acid Gas.

If, as would appear to be probable, the E.M.F. of the current of rest of the skin of the Eel, is the result of secretory processes occurring in its glandular elements instead of a "mucin-metamorphose" of the ordinary epidermic cells, it should be possible by experimental treatment to obtain increments and decrements of the E.M.F. according as the active processes are stimulated or depressed. The first experiments in this direction were made with carbonic acid gas. Engelmann (13) obtained enormous falls of the E.M.F. of the skin of the Frog by the use of this reagent, and also saw that upon replacing the CO_2 by air the original level of potential was rapidly regained. He associated this fall of E.M.F. with the contraction of the skin glands, which he had previously noticed to occur when the skin or membrana nictitans was subjected to the action of this reagent. In the skin of the Eel there are no contractile elements similar to the muscle cells which Engelmann (17) describes as sheathing both varieties of skin glands in the Frog, so that it becomes a rather simpler matter to determine upon what elements of the skin a reagent affecting E.M.F. exerts its action.

The CO_2, prepared from marble by the action of HCl, was washed with water and saturated solution of sodic carbonate, and then passed as required into the gas chamber containing the skin in contact with its electrodes.

As has been already mentioned the outer surface of the skin of the Eel *immediately* after removal may be either negative or positive to the inner surface, though, if time be given, it is the rule that the condition of outer surface negative to inner is that which finally obtains. It is therefore necessary to observe the action of CO_2 upon the E.M.F. of the skin current in both of these conditions.

The following two experiments are illustrative. In Experiment A the gas was applied to a piece of skin in the normal condition, *i.e.*, with outer surface negative to inner, while in Experiment B a case was selected where, at the commencement, the outer surface was positive, though, as is the rule, it was gradually passing towards the normal state.

N.B.—In these and in all subsequent experiments—

A *north* galvanometer deflection (N.) signifies outer surface negative to inner;
A *south* galvanometer deflection (S.) signifies inner surface negative to outer.

Experiment A.

Freshly removed Eel's skin led off from inner and outer surfaces.

Outer surface negative to inner. Deflection of galvanometer N.

The numbers in the right hand column indicate compensator degrees of which 1 = ·000008 D.

11.25 A.M.	250 N.	
11.28	200 N.	
11.30	180 N.	
CO_2 introduced into gas chamber.		
11.30½ A.M.	0	
11.31½	120 S.	Reversal of current.
Air circulated and CO_2 expelled.		
11.34 A.M.	0	
11.39	90 N.	Return to normal direction of current.
11.44	130 N.	
11.49	100 N.	
11.58	70 N.	
CO_2 again introduced.		
12.0 noon.	70 S.	Reversal of current.
Air circulated and CO_2 expelled.		
12. 3 P.M.	90 N.	Return to normal direction of current.
12. 8	40 N.	
12.30	0	

Experiment B.

Freshly removed Eel's skin led off from inner and outer surfaces.
Outer surface positive to inner. Deflection of galvanometer S.
The numbers in the right-hand column have the same unit as in Experiment A.

2.47 P.M.	440 S.
2.51	350 S.
2.55	320 S.
2.56	CO_2 introduced into the gas chamber.
2.57	390 S.
2.58½	260 S.
3. 4	250 S.
Air circulated and CO_2 expelled.	
3.10 P.M.	120 S.
3.11	CO_2 again introduced.
3.13	150 S.
3.15	190 S.
Air circulated and CO_2 expelled.	
3.17 P.M.	120 S.
3.18	50 S.
3.20	25 N. Reversal.
3.25	CO_2 again introduced.
Second reversal occurred. Deflection now again S.	
3.26 P.M.	200 S.
Air circulated and CO_2 expelled.	
3.28 P.M.	150 S.
3.30	100 S.
3.32	50 S.
3.35	10 S.
3.40	100 S.
3.43	150 S.
3.46	170 S.
3.50	200 S.

With reference to Experiment A it will be noticed that the exposure of the skin with normal direction of current to the action of CO_2 leads to a diminution of the E.M.F., and finally to a temporary reversal of the direction of the current. A recovery occurs upon the admission of air, but it is not in this case complete, for, as will be seen by reference to the earlier stages of the experiment, a general fall of E.M.F. is taking place, hastened later on no doubt by the action of the gas. In fact the precipitations of E.M.F. induced by the CO_2 are seen to be imposed upon a gentle curve of descent.

If, on the other hand, Experiment B be examined, a case where at the commencement the outer surface is positive to the inner, the following points will be evident. In the first place the negativity of the inner surface is diminishing, a fact that has already been alluded to in a previous section of this paper. In the second place the exposure of the skin to the action of the CO_2 leads, in contradistinction to the former normal case of Experiment A, to an augmentation of the E.M.F. of the current in contra-normal direction, but, as before, upon the admission of air the effect is cut out, and the ordinary diminution of negativity of the inner surface continues. In the third place it is seen that though the skin lay for 8 minutes in CO_2, at the first application, recovery from the effect was noticed within 2½ minutes, *while the skin was still subject to the action of the gas,* and the effect was relatively a small one, while in the third application, though the action was only allowed to continue for 1 minute a far greater effect was produced, suggestive of a diminution of vital resistance, though the rapid admission of air excluded any observation as to whether recovery could have still occurred while the gas was still present. Finally it is evident that the repeated exposure to CO_2 has put an end to the general tendency to replacement of negativity of inner surface by negativity of outer, for the state of matters at the end of the experiment is the reverse of that at the beginning, viz., the negativity of the inner surface is now apparently increasing.

It has been suggested that in a piece of freshly removed skin one has two opposing sources of E.M.F. at the two surfaces, the one, due to injury of the inner surface, and tending to diminish with time, the other due to the activity of secretory protoplasm situated nearer the outer surface, finally also tending to diminish, yet capable of increase, either as a result of recovery from shock of removal or on account of excitation, as will be shown later.

Upon which of these sources does CO_2 exert its action, and of what nature is that action?

It is not probable that CO_2 has any action upon the inner surface, for as far as is known CO_2 is without effect upon the electrical condition of connective tissue fibre. DU BOIS (18) has shown that short exposure of muscle to CO_2 has no appreciable effect upon the demarcation current, an experiment that I have often repeated, leading off from the tendon and belly of the gastrocnemius of the Frog, with confirmatory result. In this case, if the current is not affected, there is action upon neither muscle nor tendon, the absence of action upon the former being probably associated with the fact that the muscle tissue is, so to speak, habituated to the presence of this gas. This is not, at any rate to like extent, the case with the protoplasmic structures at the outer surface of the skin, and it is reasonable to suppose that the action of CO_2 is almost exclusively upon this surface.

With the assumption that CO_2 acts principally, if not exclusively, upon the structures of the epidermis, and that its action is, by lessening vital action, to cause a diminution of the E.M.F. dependent upon such action, the facts arising out of experiment became easily explicable.

In the normal case (Experiment A) the application of CO_2 causes, first a reduction of the E.M.F. of the outer surface to such a degree that it is balanced by that of the inner, so that there is no current, and by a continuance of its depressant action, allows the E.M.F. generated at the inner surface (probably as the result of injury during removal) to gain the upper hand, with the result that a current sets in in the reverse direction to normal. Aëration brings back activity to the protoplasm of the cells of the outer surface, and with renewed action the negativity of injury of the inner surface is again over-compensated, leading to a re-reversal of current back to normal.

Turning to the second case (Experiment B), where, whether from interference with the activity of the cells at the outer surface, or greater injury in removal to the inner, the inner surface is negative to the outer, the same explanation will hold good. The balance is here in favour of the E.M.F. of the inner surface, hence any reagent, such as CO_2, diminishing the activity of the protoplasm of cells at the outer surface that generate an opposing E.M.F., will lead to an increase in the original outgoing current, followed by a decrease when air is readmitted. In this case too a more permanent depression seems to have been produced by the action of the gas, for after the third admission of air, the general recovery that had been progressing throughout the experiment is no longer visible, but, on the other hand, has given place to a condition in which the E.M.F. of the inner surface is apparently gaining the upper hand. It is interesting to note that in the early part of the experiment the cells of the outer surface are far more resistant to the action of the CO_2 than later, for recovery occurs while the skin is actually in the gas.

The explanation offered then of the action of CO_2 upon the current of the skin of the Eel, is that by depressing the activity of protoplasmic structures in the epidermis (presumably the secretory cells) it lessens the E.M.F. constantly being generated therein by vital processes.

ACTION OF THE VAPOUR OF CHLOROFORM.

The effect of chloroform vapour upon the E.M.F. of the skin of the Frog was observed by ENGELMANN (13) to be very similar to that of CO_2. I have repeated ENGELMANN'S experiments, and am able to confirm the results he obtained.

In the experiments with the skin of the Eel the vapour was introduced into the gas chamber containing the skin by means of gentle pressure upon a rubber ball connected with a large vessel containing a sponge soaked in the drug.

The effect of chloroform vapour upon the E.M.F. of the skin of the Eel is of the same nature as that exerted by CO_2, but, as might be expected, the action of chloroform is the more powerful of the two.

If the outer surface of the skin is negative to the inner (normal condition), chloroform vapour reduces the E.M.F. of the ingoing current till the two surfaces are equipotential, and, if the action be allowed to continue, the ingoing is replaced by an outgoing current.

The replacement of the chloroform vapour by air causes a diminution of the outgoing current, and, if the action of the vapour has been short, the normal condition of an ingoing current is soon again attained.

On the other hand, should the inner surface of the skin be negative to the outer at the commencement of the experiment, then, as with CO_2, the immersion in chloroform vapour leads to an increase in the E.M.F. of the outgoing current.

The following experiment is illustrative of the action of chloroform upon the E.M.F. of a piece of skin with normal direction of current:—

Experiment C.

Freshly removed Eel's skin led off from inner and outer surfaces.

Outer surface negative to inner.—Deflection of galvanometer N.

The numbers in the right-hand column indicate compensator degrees, of which 1 = ·00008 D.

12.32 P.M.	100 N.	
12.35	140 N.	
12.38	150 N.	
12.41	180 N.	
12.44	200 N.	
12.47	220 N.	
12.49	Chloroform vapour passed into gas chamber.	
12.50	50 N.	
12.50½	Reversed current.	Deflection S.
12.51½	170 S.	
12.52	Air admitted.	
12.53½	0	Skin surfaces equipotential.
12.54	Re-reversal.	Deflection N.
12.56½	90 N.	
12.58	110 N.	
1.0	120 N.	

It is to be noticed that, though the E.M.F. of the ingoing current is rising rapidly at the commencement of the experiment, the immersion of the skin in chloroform vapour causes a precipitate fall, leading finally to a complete reversal of current.

Recovery occurs upon the admission of air, but the E.M.F. of the outer surface never attains its original maximum, though the skin was only in the vapour for 3 minutes, and was perfectly fresh.

The rapidity of recovery upon removal of the vapour is as striking in this case as it is with CO_2. By prolonging the action of the vapour, however, the recovery is found to be slower, and may be delayed for some time after the admission of air.

On the other hand, if the action of the vapour is prolonged even further, recovery may actually occur while the skin is still subjected to it.

In the following experiment the skin was left in chloroform vapour for successive periods of 5, 10, and 30 minutes, and it will be seen that, though recovery occurs immediately upon admission of air in the first case, in the second case a period of about 3 minutes elapses, while, in the third case, after the maximum effect has been produced, a period, during which there is no change of potential, occurs, and, finally, recovery commences after some 12 minutes' immersion, while the skin is still subject to the action of the vapour.

Experiment D.

Freshly removed Eel's skin led off from inner and outer surfaces

Outer surface positive to inner. Deflection of galvanometer S.

The numbers in the right hand column indicate compensator degrees of which 1 = ·000008 D.

	3.42 P.M.	500 S.	
	3.45	150 S.	
	3.46	80 S.	
	3.49	200 N.	Reversal.
	3.51	410 N.	
	3.52½	450 N.	
	3.54	420 N.	
	3.55	Chloroform vapour applied.	
	3.57	200 N.	
	4.0	50 N.	
Air admitted.			
	4.3 P.M.	140 N.	
	4.6	130 N.	
	4.9	80 N.	
	4.10	Chloroform vapour applied.	
	4.11	Faint N.	
	4.14	50 S.	Reversal.
	4.17	120 S.	
	4.20	190 S.	
Air admitted.			

4.23 P.M.	220 S.
4.26	180 S.
4.29	150 S.
4·32	145 S.
4.33	Chloroform vapour applied.
4.35	150 S.
4.38	180 S.
4.41	230 S.
4.44	230 S.
4.47	220 S.
5.3	160 S.

If chloroform vapour be applied to a skin whose current is in the contra-normal direction, *i.e.*, outgoing, the effect is similar to that already seen in the case of CO_2. Under these conditions an increase in the outgoing current takes place attributable to a diminution in the E.M.F. of the opposing ingoing current. A case of this is seen in the commencement of Experiment O, p. 362.

If the vapour of chloroform be applied exclusively to the outer or inner surface of the skin, it then becomes evident that it is upon the former almost exclusively that its action is exerted. In the following experiment a stream of chloroform vapour was gently directed upon the surface of the skin in the region of the electrode. A blank experiment with electrodes only showed that there was no appreciable galvanometer deflection from cooling of electrodes.

Experiment E.

Freshly removed Eel's skin led off from inner and outer surfaces.

Outer surface negative to inner. Deflection of galvanometer N.

The numbers in the right hand column indicate compensator degrees, of which 1 = 000008 D.

2.18 P.M.	255 N.
2.20	265 N.

Chloroform vapour applied to *Inner* surface.

2.21 P.M.	270 N.
2.22	270 N.

Chloroform vapour applied to *Outer* surface.

22.3 P.M.	250 N.
22.4	270 N.
22.5	268 N.

Chloroform vapour applied to *Inner* surface.

2.26 P.M.	270 N.
2.27	268 N.

Chloroform vapour applied to *Outer* surface.

2.28 P.M.	225 N.
2.29	270 N.

The results then of the action of chloroform vapour upon the electromotive phenomena of the current of rest of Eel's skin, seem to be capable of the same explanation as that offered in the instance of the action of CO_2, viz., that the reagent leads to a diminution of the activity of the processes going on in the secretory structures of the epidermis, with a concomitant fall in E.M.F.

It must here be mentioned that chloroform vapour may act in quite an opposite manner upon the skin of an *intact Eel* to that in which it works upon a piece of *removed skin.* A reflex copious secretory action occurs when a pithed Eel is subjected to the vapour, and the histological features of the skin of such an animal give clear indications of the process; these features are absent when the chloroform is applied to exsected skin.

It seemed of interest in connection with the action of chloroform vapour upon the skin to test the effect produced upon the demarcation current of muscle, for here, unlike the case of CO_2, which is hardly a foreign substance to muscle, one would expect to get a marked result.

The results lend some support perhaps to the theory of the action of chloroform upon the skin of the Eel just stated, for it is found that an increase in the positivity or decrease of the negativity of a contact upon the surface of a muscle occurs as the result of exposure to chloroform vapour.

Three cases are quoted below in illustration. In the first, a muscular surface made negative by section became positive when the muscle was surrounded with chloroform vapour. In the second, the contact on the belly of a removed muscle which was positive to that on the tendon, became more so from treatment with chloroform vapour, but recovered completely later. In the third case, an instance is taken where the belly of the muscle was weakly negative to the tendon, and in this case a reversal and development of a strong opposing current with belly positive to tendon resulted from the action of the vapour.

These results were obtained by the application of a vapour weak in chloroform. If, on the other hand strong vapour is pumped directly on to the muscle, the results are not constant, for injury currents from coagulation of the muscle substance are then originated.

(i.) *Gastrocnemius of Frog led off from artificial section and tendinous end.*

10.38 A.M. E.M.F. of Demarcation current ·03032 D. Cut end negative. Deflection N.

Chloroform vapour passed into the gas chamber.

10.39 A.M. *Current reversed. Cut end positive.* Deflection S.

Air circulated,
10.42 A.M. E.M.F. of reversed current ·0356 D.
10.55 „ „ ·0312 D.

(ii.) *Gastrocnemius of Frog led off from longitudinal surface and tendinous end.*

11.5 A.M. E.M.F. of Demarcation current ·0184 D. Muscle surface positive.
Deflection S.
11.6 E.M.F. of Demarcation current ·0168 D.
Chloroform vapour passed into the gas chamber,
11.7 A.M. E.M.F. of Demarcation current ·0280 D. Deflection S.
11.8 „ „ ·0192 D.
11.9 „ „ ·0168 D.

(iii.) *Gastrocnemius of Frog led off from longitudinal surface and tendinous end.*

11.20 A.M. E.M.F. of Demarcation current ·004 D. Muscle surface negative.
Deflection N.
Chloroform vapour passed into gas chamber,
11.21 A.M. *Current reversed. Muscle becomes positive.* Deflection S.
E.M.F. ·0368 D.
11.21½ „ ·0312 D. Deflection S.
11.22 „ ·0296 D. „
11.27 „ ·0232 D. „

It is evident that in all the above cases the action of the chloroform vapour was to cause diminution of negativity or increase of positivity of the muscular substance, *i.e.*, the same effect as that produced upon the outer surface of the Eel's skin.

EXCITATION.

In the above pages, the experiments quoted have dealt solely with depressions of the value of the E.M.F., generated at the outer surface of the skin. It is now necessary to turn to the question whether it may not be possible to obtain increments of E.M.F. as a result of excitation.

Excitatory electrical variations in glandular structures have long been known. VALENTIN (19), in 1861, and ROEBER (20), in 1869, demonstrated the fact for the skin of the Frog. HERMANN and LUCHSINGER (21), in 1878, did the same in the case of the tongue glands of the Frog and the sweat glands of the paw of the Cat, LUCHSINGER (22), in 1880, in the glands of the snout of the Pig, Goat, and Cat, and BAYLISS and BRADFORD (16), in 1887, in the salivary glands of the Cat and Dog.

The case of the skin of the Frog has been more frequently examined than the others, but the results have proved most conflicting at the hands of the several observers

The conditions here which appear to affect the nature of the electrical variation upon excitation of the cutaneous nerves are numerous. They are given as follows by the different authors. The magnitude of the original current of rest (ROEBER, HERMANN, BACH, and OEHLER). The state of humidity of the surface of the skin (ROEBER and ENGELMANN). The strength of the stimulus (HERMANN, ENGELMANN, BACH, and OEHLER, and BAYLISS and BRADFORD). The temperature of the skin (BACH and OEHLER). The time that has elapsed since the commencement of the experiment (BACH and OEHLER). Finally, the condition of the animal, with special reference to that obtaining during the breeding season (BAYLISS and BRADFORD).

On the whole, perhaps, the mass of the evidence seems to point in favour of a diphasic variation as a result of excitation of the skin of the Frog, the first phase being negative, and the second positive. Of these two phases, the second, or positive, appears to be the more marked, the first being often spoken of as a "Vorschlag," though under various conditions of experiment the reverse is the case, so that BAYLISS and BRADFORD (14, p. 223) observe, "It is scarcely possible to speak of a normal excitatory variation." My own experiments upon the excitatory variation of the current of the Frog's skin are as yet too incomplete to justify any entrance upon a discussion of the nature of the variation in this paper; it appears, however, that the chief difficulty in predicting the variation which will follow a stimulus is associated with the great variability in the states of contraction and expansion of the skin glands, as demonstrated by ENGELMANN (17).

In the lingual glands of the Frog, HERMANN and LUCHSINGER noted, upon stimulation of both the glosso-pharyngeal and hypoglossal nerves, a strong positive electrical variation of the rest current, interrupted by a negative phase so short in duration that the positive phase outlived it, and was still able to make itself subsequently evident.

In the Cat's paw, the same observers saw that a current directed from the outer to the inner surface of the skin (corresponding to a "positive variation") was developed, as a result of excitation of the sciatic nerve.

In the glands of the snout of the Pig, Goat, Dog, and Cat, LUCHSINGER also observed a positive variation of the current of rest.

The observations of BAYLISS and BRADFORD upon the variations of the current of rest of the submaxillary glands of the Dog and Cat led them to the conclusion that "the sign of the electrical disturbance varies with the nature of the secretion, as measured by its amount and its viscidity," so that the excitation of a nerve trunk in which "secretory" fibres predominate leads to a positive variation of the rest current, whereas the stimulation of one containing an excess of "trophic" fibres leads to a negative variation.

In the glands, then, of the paw of the Cat and the snout of the Pig, Goat, Dog, and Cat, the excitatory variation observed has been purely positive, while in the Frog's tongue it has been mainly positive, but interrupted by an interpolated negative phase.

In the case of the skin of the Frog the evidence is not perfectly clear, but of the two phases of the variation the positive appears to be the more marked. Finally, in the Mammalian salivary gland, there would appear to be a definite connection between the nature of the nerve fibres stimulated and that of the electrical change.

In experiments upon excitation of the skin of the Eel it is unfortunately impossible to make use of indirect stimulation by cutaneous nerves. This fact is occasioned by the absence of a large subcutaneous lymph space, such as exists in the case of the Frog and Toad, so that a "nerve-skin preparation" is not feasible. It is, therefore, necessary to resort to direct stimulation, which may be electrical, thermic, or mechanical.

In the circuit represented in fig. 1, p. 338, it is evident that, by means of the switch C, induction shocks can be applied to the skin through the leading-off electrodes, and the current of the skin subsequently passed into the previously compensated galvanometer circuit.

With carefully made "non-polarisable" electrodes, and by reversals of the direction of the stimulating current, it is possible to assure oneself of freedom from error due to polarisation.

Whatever method of stimulation is employed, it is found, firstly, that the skin of the Eel is excitable; and, secondly, that the electrical variation is one indicative of increase in the negativity of the outer surface, *i.e.*, a positive variation, if the resting current is in the normal direction.

STIMULATION WITH SINGLE INDUCTION SHOCKS.

When a single induction shock is passed through the skin and the electrodes subsequently connected with the galvanometer, the following points are observed. Firstly, an electrical variation, indicative of increased negativity of the outer surface, occurs; secondly, the excitatory state rapidly reaches its maximum, falls quickly at first, and then very slowly. Thirdly, the amount of the primary variation is dependent upon the strength of the stimulus.

These points are illustrated by the following example:—

Experiment F.

Freshly removed Eel's skin, led off from outer and inner surfaces.

Outer surface negative.—North deflection of galvanometer.

Stimulation with break induction shock. Coil 15 centims. Positive excitatory variation. N. deflection.

Reversal of direction of stimulating current did not affect variation.

Make shock at 15 centims. coil: no effect.

Stimulation with coil at 10 *centims.*—Break shock: larger deflection than before. Make shock: no effect.

Coil at 5 *centims.*—Make shock: effective.

STIMULATION with Coil at 5 centims.

Make shock.		Break shock.	
Seconds after stimulus.	Galvanometer reading.	Seconds after stimulus.	Galvanometer reading.
0	0°	0	0°
5	45	5	230
10	30	20	120
20	20	30	60
30	15	40	50
40	12	50	40
50	10	60	35
60	8	70	30
70	8	90	22
90	7	100	20
110	6	110	17
130	3	130	15
150	2	150	11
200	0	180	8
		230	5
		260	3
		300	0

The rapid arrival of the E.M.F. of the excitatory variation at its maximum is remarkable, and, as far as my own experience goes, considerably more marked than in the case of the Frog's skin directly excited. The slowness, however, of the subsequent decline agrees closely with the phenomena of the variation of the Frog's skin, as already noted by HERMANN and BAYLISS and BRADFORD. In the case of the submaxillary gland, BAYLISS and BRADFORD mention the occurrence of a quick maximum and slow decline of potential as a result of chorda stimulation.

As regards the length of the latent period, I have as yet been unable to make any exact measurements; all that can be here stated is that it is shortened by increasing the strength of the stimulus—a fact already noticed by ENGELMANN in the case of the skin of the Frog.

The relation, too, between the magnitude of the variation and the strength of the stimulus evident in Experiment F. (where the break shock gave a deflection of 230° and the make only 45° with coil at 5 centims., while at 10 the make shock was ineffectual), has been observed by both ROEBER and ENGELMANN in the case of the Frog's skin, the former using indirect stimulation by means of the cutaneous nerves, the latter stimulating directly through the leading-off electrodes.

STIMULATION BY FARADISATION.

The excitatory effect following faradisation of the skin is, as would be expected, far more marked than that produced by the application of a single induction shock.

The increase of E.M.F. upon stimulation, as measured by the method I have used, is, of course, no criterion of that actually developed in the skin, on account of the short circuiting that occurs in the skin structures themselves, but the percentage value in terms of that of the current of rest is of interest.

Some observations of the increase of the E.M.F. upon faradic stimulation of the skin of the Eel will be found in Table I.

TABLE I.—Increase of E.M.F. of the Skin of the Eel as a Result of Faradic Excitation.

I.	II.	III.	IV.	V.	VI.
Number.	E.M.F. of current of rest.	Increase of E.M.F. following excitation.	Percentage increase of E.M.F. in terms of that of current of rest.	Stimulus.	Remarks.
1	·00128 D	·00032 D	25·0	Coil 15 for 5″	Same Eel.
2	·00320 D	·00032 D	10·0	,,	
3	00212 D	·00040 D	18·8	,,	Same Eel.
4	·00248 D	·00044 D	17·7	,,	
5	·00276 D	·00036 D	13·0	,,	
6	·00264 D	·00040 D	15·1	,,	
7	·00280 D	·00048 D	17·1	,,	
8	·00288 D	·00068 D	23·6	,,	
9	·00292 D	·00056 D	19·1	Coil 15 for 15″	
10	·00116 D	·00112 D	96·5	Coil 20 for 5″	Same Eel.
11	·00112 D	·00060 D	53·5	,,	
12	·00076 D	·00144 D	189·4	Coil 15 for 5″	
13	·00120 D	·00036 D	30·0	Coil 20 for 5″	Same Eel.
14	·00116 D	·00120 D	103·4	,,	

The method employed in obtaining these measurements, viz., compensation as rapidly as possible after stimulation, must give a value considerably below the maximum, for, as has been already noted, the rise of E.M.F. on stimulation is sudden and at first declines rather rapidly; but as will be seen in Case 12 the E.M.F. of the action current may almost double that of the current of rest; this is, however, very exceptional.

ENGELMANN observed a variation of 25 per cent. to 30 per cent. in the E.M.F. of the Frog's skin upon stimulation with a single induction shock and a variation of 40 per cent. to 50 per cent. with repeated stimuli; these variations were, however, of the nature of falls of the E.M.F. of the current of rest.

Bayliss and Bradford state that the E.M.F. of the positive phase of the variation of the Frog's skin current may exceed ·022 volt, but since they give no relative values for the E.M.F. of the current of rest this number is of little value, though taking ·1 volt as an average E.M.F. for the current of rest, an increase of 22 per cent. is a possibility.

In the case of injured muscle, Sanderson and Gotch (23) have demonstrated that the E.M.F. of the current of action may exceed considerably that of the demarcation current. In the gastrocnemius of vigorous Frogs they observed that the E.M.F. of the action current might be more than double that of the current of rest (·084 D as against ·04 D); in the sartorius, however, though the E.M.F. of the action current undoubtedly exceeds that of the demarcation current, the ratio is not so large as in the case of the gastrocnemius. These results, however, are not comparable with those stated in Table I., for not only were they gained with a single induction shock as stimulus, but the method of measurement was far more accurate than that which I have employed.

If stimulation be applied to a piece of Eel's skin, which is in the condition of outer surface positive to inner, the variation of the current of rest is negative instead of positive, for, as has been stated above, excitation always results in an increase in the negativity of the outer surface.

An instance of this is given in the following experiment.

Experiment G.

Freshly removed Eel's skin, led off from inner and outer surfaces.

Outer surface positive to inner. Deflection of galvanometer S.

The numbers in the right-hand column indicate compensator degrees, of which 1 = ·000008 D.

8.50 P.M.	350 S.
8.51	305 S.
8.52	280 S.
8.53	255 S.
8.57	195 S.
Stimulation, coil 15 for 5″.	N. variation, *i.e.*, negative.
8.58 P.M.	165 S.
9.0	135 S.
Stimulation, coil 15 for 5″.	N. variation, *i.e.*, negative.
9.1½ P.M.	95 S.
9.2	106 S.
9.3	95 S.
9.4½	85 S.
9.5	78 S.

Stimulation, coil 15 for 5″.*	N. variation, *i.e.*, negative.
9.6 P.M.	49 S.
9.7	55 S.
9.8	49 S.
9.9	35 S.

The reductions of E.M.F. which follow excitation in this experiment are obviously the result of the excitatory increase of the E.M.F. of the ingoing current, which at the time the experiment was commenced was below that of the outgoing current, though evidently gradually gaining the upper hand, as is the general rule.

When, on the other hand, the skin is in the normal condition, *i.e.*, with outer surface negative to inner, the variation upon faradisation is invariably, as far as I have seen, of a positive nature.

The following experiment is typical of the normal variation upon faradisation.

Experiment H.

Freshly removed Eel's skin led off from inner and outer surfaces.

Outer surface negative to inner. Deflection of galvanometer N.

The numbers in the right-hand column indicate compensator degrees, of which 1 = ·000008 D.

3.0 P.M.	145 N.
Stimulation, coil 20 for 15″.	N. variation, *i.e.*, positive.
3.1 P.M.	285 N.
3.4	195 N.
3.7	195 N.
3.10	185 N.
3.13	170 N.
3.16	140 N.
Stimulation, coil 20 for 5″.	N. variation, *i.e.*, positive.
3.17 P.M.	215 N.
3.17½	185 N.
3.20½	155 N.
3.23½	95 N.
Stimulation, coil 15 for 5″.*	N. variation, *i.e.*, positive.
3.24½ P.M.	275 N.
3.25	225 N.
3.28	210 N.
3.31	185 N.

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* Indicates reversal of direction of stimulating current.

The quick rise of E.M.F. upon excitation and the slow return to the previous value are clearly seen in this experiment, and also the dependence of the magnitude of increase of the E.M.F. upon the strength of the stimulus.

Since ROEBER had noticed the occurrence of fatigue phenomena in the case of the excitatory variation of the skin of the Frog, I deemed it of interest to search for evidence of the fact in the case of the Eel. Pieces of skin, the E.M.F. of whose current of rest was increasing with time, were chosen for experiment, since, if any evidence of fatigue were forthcoming as a result of repeated excitation, it would obviously be more convincing in such instances.

The following experiment is an instance of an attempt to produce a condition of fatigue.

Experiment K.

Freshly removed Eel's skin led off from inner and outer surfaces.

Outer surface negative to inner. Deflection of galvanometer N.

The numbers in the right-hand column indicate compensator degrees of which 1 = ·000008 D.

1.35 P.M.	125 N.
1.37	135 N.
1.39	155 N.
1.41	180 N.
1.43	190 N.
1.45	200 N.
1.47	215 N.
1.49	225 N.
1.51	245 N.
1.53	255 N.
1.55	265 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
1.55½ P.M.	315 N.
1.57	295 N.
1.58	300 N.
1.59	295 N.
2.1	310 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
2.1½ P.M.	365 N.
2.3	350 N.
2.5	345 N.
2.7	345 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
2.7½ P.M.	390 N.

2.9 P.M.	375 N.
2.11	370 N.
Electrodes moistened.	
2.13 P.M.	330 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
2.13½ P.M.	380 N.
2.14	360 N.
2.15	350 N.
2.17	350 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
2.17½ P.M.	410 N.
2.19	375 N.
2.21	360 N.
2.23	360 N
2.25	360 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
2.25½ P.M.	445 N.
2.26	405 N.
2.27	375 N.
2.29	370 N.
2.31	370 N.
2.32	365 N.
2.35	365 N.
2.37	365 N.
Stimulation, coil 15 for 15″.	N variation, *i.e.*, positive.
2.37½ P.M.	435 N.
2.39	410 N.
2.41	400 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
2.41½ P.M.	435 N.
2.43	410 N.
2.45	405 N.
Stimulation, coil 15 for 5″.	N variation, *i.e.*, positive.
2.45½ P.M.	445 N.
2.47	425 N.
2.49	415 N.
Stimulation, coil 15 for 60″.	N variation, *i.e.*, positive.
2.51 P.M.	470 N.
2.53	440 N.
Stimulation, coil 15 for 60″.	N variation, *i.e.*, positive.
2.54½ P.M.	490 N.

2.55 P.M. 475 N.
Coil now put to 0, and stimulation continued for 60″.
E.M.F. of current of rest 500 N.
Stimulation, coil 0 for 10″. N variation, *i.e.*, positive.
½ minute later 510 N.

It is noticeable in this experiment that in spite of the repeated stimulation, the E.M.F. of the current of rest continues to rise, and during the early period of the experiment, at any rate, there is no evidence of any diminution in the amount of the positive response to excitation. The amount of the variation is a little reduced in the case of the eighth and ninth excitations, in spite of the longer period of stimulation; but it is not till the skin has been subjected to stimulation for a period of sixty seconds, with the coil at zero, that any marked diminution in the excitatory variation becomes evident, though even then no fall in the E.M.F. of the current of rest occurs.

It would appear then, that the skin of the Eel is remarkably resistant as regards fatigue.

Whether the continuation in the rise of E.M.F. throughout this experiment is in part due to some beneficial effect of the stimulus, somewhat of the nature of the rise in the E.M.F. of the rest current of the submaxillary gland noted by BAYLISS and BRADFORD after stimulation of the sympathetic, it is difficult to decide, for in this case the E.M.F. of the current of rest was rising before the stimulation was commenced. I have attempted to convert a case of falling E.M.F. of current of rest into one of rising E.M.F., by repeated excitation, but so far without success. Any attempt to explain the continuation of increase of the negativity of the outer surface upon a hypothesis of increase in alkalinity as a result of excitation is negatived by the fact that long faradisation of pieces of skin leads to the opposite effect, *i.e.*, diminution of alkalinity of the outer surface.

THERMIC STIMULATION.

ENGELMANN obtained a negative electrical variation upon the application of heat to the skin of the Frog, using a platinum wire traversed by the current from two GROVE's cells. This is, as far as I am aware, the only case recorded of the effect of heat upon the electrical phenomena of a glandular structure.

In the case of the skin of the Eel, I applied heat by bringing a small heated copper spatula into the neighbourhood of the skin. Such a position of the electrodes was always selected that the thermo-electric variation due to heating of the electrode nearer the spatula was against any electrical variation arising in the skin itself.

I found, as in the case of electrical excitation, a pure positive variation indicative of increase in the negativity of the outer surface, in all cases where the outer surface of the skin was heated above the temperature of the inner.

The following experiment is given in illustration.

Experiment L.

Electrodes placed in contact with one another lie east and west.
Heating *west* electrode. S deflection of galvanometer.
,, *east* ,, N ,, ,,
Freshly removed Eel's skin now led off by the electrodes.
West electrode in contact with *outer* surface.
West electrode negative. *Deflection N*, E.M.F. ·00128 D.
Heated spatula held 3 to 4 centims. from *outer* surface.
N deflection, 20° of scale.
Return to zero in 2 minutes.
Heated spatula held near *inner* surface.
Faint N deflection (thermo-electric current from east electrode ?).
Repeated many times with similar result.

The positive excitatory variation (N deflection) in the case of heating of the outer surface, was evidently sufficiently strong to swamp any thermo-electric current (S deflection) due to heating of the electrode in contact with the skin.

MECHANICAL STIMULATION.

ENGELMANN has noticed that the current of rest of the skin of the Frog is subject to a negative variation upon mechanical stimulation, and I have already mentioned that the same holds good for the skin of the Toad. Indeed, the skin of the Toad is even more sensitive to this kind of stimulus than that of the Frog, the slightest pressure with a glass pointer, and without any possibility of shifting of the thread electrodes, leading to a diminution of the negativity of the electrode in the neighbourhood of the stimulated spot.

Two electrodes on the outer surface of the skin of a Toad spread on glass.

	Electrode A.	Electrode B.
First reading	+	–
1′ later, spontaneous change to	–	+
Fall of potential, marked by irregularities, to . .	0	
4″ later, reversal to	+	–
Pressure near B change to	–	+
,, ,, A ,, back to.	+	–

The above is an extreme case, and is not only noticeable for the complete reversal of sign upon irritation, but also for the spontaneous reversal and re-reversal at the commencement of the experiment. With the glands of the "ear swellings" I have obtained similar results.

With the skin of the Eel, I have exclusively obtained a variation indicative of increased negativity of the spot excited upon mechanical stimulation. It is, of course, impossible to apply mechanical stimulation with safety, when the skin is on the cork frame and led off from the inner and outer surfaces, on account of the danger of shifting the electrodes. It is necessary to spread the skin upon a glass plate with the outer surface uppermost, and then stimulate by pressure with a fine glass pointer with knobbed extremity in proximity to one electrode.

The following experiment is an instance of mechanical excitation :—

Experiment M.

Freshly removed Eel's skin led from two points on the outer surface. E.M.F. of current of rest ·000768 D. Deflection S.

Electrode A.	Electrode B.
+	–

Slight pressure near B. S deflection of 23°, *i.e.*, increased negativity of B.
Return to zero not complete.
Rest current recompensated.
Slight pressure near A. N deflection 20°, *i.e.*, increased negativity of A.

The variation, therefore, upon mechanical stimulation corresponds to that obtained when excitation is electric or thermic.

Any discussion as to the reason of the opposite nature of the variations in the Batrachian skin on the one hand, and in the Fish skin on the other, in the cases of both direct electrical and mechanical excitation, is out of place in this paper ; it must, however, be here noted, that though the excitatory variation in the skin of the Eel is invariably such as to indicate increased negativity of the outer surface, pure and simple, *i.e.*, a positive variation with normal direction of the current of rest, the variation upon direct excitation of the skin of the Frog and Toad is often not purely negative, but presents a second positive phase, preceded by a negative "Vorschlag" similar to that obtained upon nerve excitation, and already noted by HERMANN, BACH and OEHLER, and BAYLISS and BRADFORD.

ACTION OF ATROPINE.

The Eel appears to be extraordinarily resistant to intoxication with atropine. It is, of course, impossible to employ subcutaneous injection, for the animal cannot be handled for the purpose if regard is to be had for the integrity of the epidermis.

Atropinisation has therefore to be effected by adding the drug to the water in which the animal is placed. TIEGEL (24) has used this method with success for the purpose of intoxication of Eels with strychnia, obtaining evidence of absorption of the drug in one and a-half hours when six milligrammes of strychnia were added to the litre and a-half of water in which the Fish was swimming. I have kept Eels for two days in ·15 per cent. solution of atropine sulphate aërated by a Bunsen pump, with apparently little effect as regards general vital phenomena. The animals were lively at the end of this period, and though the pupil was slightly dilated it reacted to light, yet chemical tests applied to proteid free watery extracts of the livers showed that atropine had been absorbed.

The removed skins of such atropinised Eels are found to give either a very feeble ingoing current of rest or outgoing currents which do not reverse with time. This fact is perhaps best explained upon the hypothesis that atropine diminishes the activity of the glandular preparatory processes, and is of interest in connection with the statement by BAYLISS and BRADFORD that the E.M.F. of the current of rest of the skin of the Frog is reduced by treatment with atropine.

When the skin of an atropinised Eel is subjected to stimulation by means of the break induction shock, it is found that the normal excitatory variation can no longer be obtained, provided the atropinisation is sufficient.

The following experiment is illustrative of this fact.

Experiment N.

Eel allowed to live in ·15 per cent. solution of atropine sulphate for 48 hours. Pupil slightly dilated but reacted to light. Skin removed immediately after pithing and led off from outer and inner surfaces. *Outer Surface negative to inner.* Deflection N. The figures in the right hand column indicate compensator degrees of which 1 = ·000008 D.

5.10	130 N.
5.13	113 N.
5.15	85 N.
5.16	Stimulation, break induction shock, coil 15. No effect.
5.17	75 N.
5.18	60 N.
5.19	Stimulation, break induction shock, coil 10. No effect.
5.20	60 N.
5.21	Stimulation, break induction shock, coil 5. No effect.
5.24	35 N.
5.25	20 N.
5.26	Stimulation, break induction shock, coil 0. No effect.
5.42	Current reversed. Outer surface +. S. deflection. 55. Stimulation, break induction shock, coil 0. No effect.

Liver and skin extracted with water for 17 hours at 40° C. Extract freed from proteid by saturation with ammonium sulphate, evaporated with HNO_3 to dryness and alcoholic soda added, reddish-violet reaction, presence of atropine.

The abolition of the excitatory variation by atropine lends considerable support to the glandular hypothesis of origin of its E.M.F.

Exclusion of the Excitatory Variation by Narcotisation.

It has been seen that by means of CO_2 and also by the vapour of chloroform, the negativity of the outer surface of the skin of the Eel may be diminished; while, by electrical, thermic, and mechanical stimulation it may be increased, so that, according to the sign of the outer surface of the skin at the moment that it is the subject of experiment, a variation is induced which, in the normal state of outer surface negative to inner, is negative with the depressants and positive with excitation; while, should the inner surface be negative to the outer, the reverse is the case.

Thus:—

	Sign of variation.		
	CO_2.	Chloroform.	Excitation.
(*a.*) Outer surface of skin negative to inner surface (normal) . . .	−	−	+
(*b.*) Outer surface of skin positive to inner surface	+	+	−

The fact that in skin with normal direction of rest current, the E.M.F. may be brought down to zero by chloroform, and by continued action a reversal of current occasioned, so that the inner surface is negative to the outer, but that recovery to the normal is possible upon readmission of air (*vide* Experiment C, and Experiment O) is very strongly in favour of the source of the E.M.F. of the normal current of rest being in some vital processes going on near the outer surface whose activity can be temporarily reduced by narcotisation.

That it is one and the same set of vital processes that is acted upon, in the direction of augmentation by excitation, and diminution by the presence of a narcotic, is shown by the interesting fact that it is possible to narcotise the skin with chloroform vapour, with accompanying diminution in the negativity of the outer surface, to such a degree that it absolutely fails to give a positive response to stimulation by electricity during the continuance of the narcotisation, though removal of the vapour allows of complete recovery.

The following experiment is illustrative of this point in particular:—

Experiment O.

Freshly removed Eel's skin led off from inner and outer surfaces.

Outer surface positive to inner.—Deflection of galvanometer S.

The figures in the right-hand column indicate compensator degrees, of which 1 = ·000008 D.

3.47 P.M.	415 S.
3.49	295 S.
3.51	195 S.
3.52	175 S.

Stimulation, coil 15 for 5″ N deflection, *i.e.*, negative variation.

3.53 P.M.	125 S.
3.55	85 S.
3.56	75 S.

Chloroform vapour passed into gas chamber.

3.57 P.M.	205 S.

Air admitted.

3.58 P.M.	150 N, *i.e.*, reversal to outer surface negative.
4.1	130 N.

Chloroform vapour passed into gas chamber.

Reversal so that outer surface now again positive.

4.3 P.M.	75 S.

Air admitted.

Reversal again to condition of outer surface negative.

4.5 P.M.	195 N.
4.7	170 N.

Stimulation, coil 15 for 5″. N deflection, *i.e.*, positive variation.

4.7½ P.M.	215 N.
4.9	185 N.

Chloroform vapour passed into gas chamber.

4.11 P.M.	15 N.

Stimulation, coil 15 *for* 5″ *while in chloroform vapour. No effect.*

Air admitted.

4.13 P.M.	35 N.
4.17	95 N.
4.19	225 N.
4.24	255 N.

CO_2 passed into gas chamber.

Reversal to outer surface positive.

4.26 P.M.	40 S.

Stimulation, coil 15 for 5″ in atmosphere of CO_2. N deflection.

4.26½ P.M.	25 S.
Air admitted.	
Reversal to outer surface negative.	
4.30 P.M.	65 N.
4.32	155 N.
4.35	185 N.

The early part of this experiment illustrates points already referred to, viz., the action of electrical stimulation and of chloroform vapour upon the skin in the condition of outer surface positive to inner. The main point of interest is seen between the times of 4.7 and 4.24. It will be noted that the same stimulus which at 4.7 liberates a positive variation of the rest current while the skin is in the normal condition, at 4.11, when the skin is under the influence of chloroform vapour, *is unable to produce any effect.* This is not due to any permanent depression of vitality, for it will be noticed that by 4.24 the E.M.F. of the current of rest is considerably above the level at which it stood at 4.7. It is also to be noted that with CO_2 the same degree of narcotisation is not produced, for, in this case (4.26), the skin is still able to respond to the stimulus, though not to such good effect as before.

CONCLUSION.

In the foregoing pages it has been demonstrated that an electromotive force is developed as a result of excitation of the skin of the Eel, which manifests itself as an increase of the negativity of the normally negative outer surface. Is this E.M.F. to be rightly considered as due to an increase in the activity of the glandular preparatory processes, to whose charge that of the normal rest current has been laid, or are the E.M.F. of the current of rest and that of the current of action of different origin ?

HERMANN, in his explanation of the negative "Vorschlag" and positive after variation of the Frog skin current as a result of indirect excitation, has assumed, mainly upon the ground of his results with the Fish skin, that the E.M.F. of the current of rest is mainly epidermic in origin, while that of the action current is glandular.

It has been seen that an epidermic origin for the E.M.F. of the rest current of the Eel's skin upon the theory of mucin-metamorphosis will not hold good, and that it is far more probable that the explanation that the source of the E.M.F. of the current of rest is in the preparatory processes going on in glandular structures, is the correct one. If such be the case, the most simple explanation of the origin of the E.M.F. of the current of action in the Eel's skin is that it is simply due to an increase in the activity of processes whose molecular changes give rise to that of the current of rest. Most striking support is given to this explanation by the fact, evident in Experiment O, that, when the E.M.F. of the rest current is reduced nearly to zero by the action of chloroform vapour, the normal excitatory development of E.M.F. is absent.

It remains now to recapitulate a few of the more important points with reference to the electromotive properties of the skin of the Eel dealt with in this paper:

1. The assumption that the E.M.F. of the current of rest of the skin of the Fish is entirely due to epidermic mucin-metamorphosis, and that it is not possible to attribute it to the presence of glandular elements, is negatived, in the case of the Eel, by the absence of any such mucinous change in the superficial epidermic cells, and by the presence of abundance of secretory cells throughout the structure.

2. The existence of considerable differences of potential between two contacts upon the outer surface of the skin, and the fact that such electromotive force is capable of excitatory increase upon mechanical stimulation, coincides with the assumption that the E.M.F. of the current of rest is the outcome of glandular processes of variable activity, and is not compatible with the theory of origin of the E.M.F. in mucin-metamorphosis.

3. The reductions in the E.M.F. of the normal rest current following exposure of the skin to carbonic acid gas and to the vapour of chloroform, and the subsequent recovery upon admission of air, are strong evidence that the origin of the E.M.F. is in some active vital processes taking place in the skin, and it is reasonable to assume that these occur in its glandular elements.

4. The demonstration that the E.M.F. of the skin of the Eel undergoes an excitatory variation as a result of electrical, thermic, and mechanical stimulation, is in accordance with what is known to occur in other glandular structures, and the fact that such excitatory change manifests itself as a positive variation of the current of rest agrees in the main with the phenomena observed in other cases.

5. The fact that chloroform narcosis excludes the possibility of the excitatory variation upon stimulation at the same time as it reduces the E.M.F. of the normal current of rest to zero, supports the assumption that the E.M.F. of the current of rest and that of the current of action originate in one and the same source.

6. Finally, the reduction of the E.M.F. of the normally directed current of rest by atropinisation, and the complete absence of any excitatory variation under such conditions, are facts strongly in favour of the hypothesis that both the E.M.F. of the current of rest and that of the current of action are from a glandular source.

BIBLIOGRAPHY.

1. HERMANN. Neue Untersuchungen über Hautströme. PFLÜGER'S Archiv, vol. 27, 1882, p. 280.
2. DU BOIS-REYMOND. Untersuchungen über thierische Elektricität, vol. 2, Abth. 2, p. 9–20.
3. HERMANN. Über die Secretionsströme und die Secretreaction der Haut bei Fröschen. PFLÜGER'S Archiv, vol. 17, 1878, p. 291.

4. Bach und Oehler. Beiträge zur Lehre von den Hautströmen. Pflüger's Archiv, vol. 22, 1880, p. 30.
5. Rosenthal. Über das elektromotorische Verhalten der Froschhaut. Reichert und Du Bois-Reymond's Archiv, 1865, p. 301.
6. Leydig. Über die Haut einiger Süsswasserfische. Zeitsch. f. wissensch. Zoologie, vol. 3, 1851, p. 1.
7. Leydig. Hautdecke und Hautsinnesorgane der Fische. Halle, 1879.
8. F. E. Schulze. Epithel- und Drüsen-Zellen. Arch. f. mikr. Anat., vol. 3, 1867, p. 137.
9. Foettinger. Recherches sur la structure de l'épiderme des Cyclostomes, etc. Bulletin de l'Académie royale de Belgique, 2^{me} série, vol. 41, 1876, p. 599.
10. List. Zoolog. Anzeiger, Jahrg. 8, 1885, p. 388.
    Biologisches Centralblatt, vol. 5, 1885–6, p. 698.
    Archiv f. mikr. Anat., vol. 27, 1886, p. 481.
11. Kölliker. Würzburger naturwissensch. Zeitschrift, Hft. 1, 1860.
12. Hoyer. Über den Nachweis des Mucins in Geweben mittelst der Färbemethode. Archiv f. mikr. Anat., vol. 36, 1890, p. 310.
13. Engelmann. Die Hautdrüsen des Frosches. Pflüger's Archiv, vol. 6, 1872, p. 97.
14. Bayliss and Bradford. On Electrical Phenomena accompanying Secretion in the Skin of the Frog. Journal of Physiology, vol. 7, p. 217.
15. Budge. Über den galvanischen Strom, welcher sich in der Haut des Frosches zu erkennen giebt. Poggendorff's Annalen, 1860, p. 537.
16. Bayliss and Bradford. The Electrical Phenomena accompanying Secretion. Internat. Monatsschrift für Anat. u. Physiol., vol. 4.
17. Engelmann. Die Hautdrüsen des Frosches. Pflüger's Archiv, vol. 5, 1872, p. 498.
18. Du Bois-Reymond. Untersuchungen, vol. 2, Abth. 1, p. 187.
19. Valentin. Zeitsch. f. rat. Med., vol. 15, 1861, p. 208.
20. Roeber. Über das elektromotorische Verhalten der Froschhaut bei Reizung ihrer Nerven. Reichert und Du Bois-Reymond's Archiv, 1869, p. 633.
21. Hermann und Luchsinger. Über die Secretionsströme der Haut bei der Katze. Pflüger's Archiv, vol. 17, 1878, p. 310.
    Hermann und Luchsinger. Über Secretionsströme an der Zunge des Frosches. Pflüger's Archiv, vol. 18, p. 460.
22. Luchsinger. Neue Beiträge zur Physiologie der Schweiss-secretion. Pflüger's Archiv, vol. 22, 1880, p. 152.
23. Burdon Sanderson and Gotch. Journal of Physiology, vol. 12, No. 4.
    Proceedings of Physiological Society. Oxford, June 20, 1891.
24. Tiegel. Vom Rückenmark der Schlangen und der Aale. Pflüger's Archiv, vol. 17, 1878, p. 594.

V. *The Cerebrum of* Ornithorhynchus paradoxus.

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[Plates 20–22.]

Summary.

The brain of *Ornithorhynchus* is completely devoid of convolution, simple in structure, and similar in many respects to the brains of the embryos of higher Mammals. It is, however, strictly Mammalian and not Avian in type.

It differs from most, if not from all, other Mammalian brains in many respects, of which the following are the most notable :—

It is destitute of corpus callosum; the structure which has been described under this name is limited exclusively to the hippocampus, and belongs therefore to the fornix. It forms a decussation or commissure above the anterior commissure. Fibres reach this decussation from all parts of the hippocampus, both in front and behind. The fibres from the decussation turn downwards in three sets (1) in front of the anterior commissure; (2) between the anterior commissure and the soft commissure; (3) above the soft commissure.

The hippocampus extends to the extreme anterior end of the hemisphere above the ventricle.

The rhinencephalon (pyriform lobe, natiform protuberance, &c.) extends at first along the base and afterwards along the mesial aspect of the hemisphere to the posterior extremity of the ventricle.

In the absence of the corpus callosum and septum pellucidum the cortex of the mesial wall of the hemisphere is continuous through the anterior perforated substance with the corpus striatum.

In a similar manner the putamen of the nucleus lenticularis is continuous, behind the cerebral crus, with the cortex of the rhinencephalon. Appearances therefore suggest that nucleus caudatus and putamen belong to the mesial wall of the hemisphere which has been involuted by the crus, the optic thalamus, and perhaps by the remainder of the nucleus lenticularis.

Historical.

The brain of the *Ornithorhynchus*, like all other parts of the animal, is very elaborately and beautifully figured in MECKEL's monograph.[*] He represents correctly the pyriform shape of the hemispheres; their surface perfectly smooth save for the deep grooves cut by the blood-vessels which, emerging from beneath the outer sides of the olfactory bulbs, radiate backwards. MECKEL does not appear, however, to have noticed the middle cerebral artery. He figures the blood-vessels which groove the internal surface of the hemisphere, as well as the deep groove which is continued forwards from above the hippocampus to the anterior extremity of the brain. The figure of a sagittal section in the median plane (Plate 7, fig. 7) is drawn with great accuracy, but the references to the figure are singularly incorrect, so incorrect, in fact, that we should infer that the pointer-lines were wrongly placed by the engraver if their disposition did not agree entirely with the description in the text. As the mistakes are made with regard to just those features which are, owing to the position of this animal amongst vertebrates, of highest importance, it is necessary to quote the words of the text in connection with the lettering of the figures. In the figure the hippocampus or ridge produced by the projection of the fascia dentata is called the "corpus callosum." The transverse commissure, which seems to take the place of the corpus callosum, is lettered as the "septum pellucidum." That there is no mistake in the lettering of the figures is evident from the following description of the former structure[†]:—"Corpus callosum adest quidem, sed breve, quum haud quatuor lineas longitudine aequet. Memorabilius etiam videtur, in dimidia duo lateralia, linea mediana haud confluentia, esse disjunctum. Equidem saltem in faciebus sese spectantibus internis nullum dilacerationis vestigium invenire potui."

As MECKEL makes no reference in the text to the structure which he figures as the septum pellucidum, it is impossible to tell how it came about that a large transverse commissure was thus named.

OWEN's description[‡] is even less easy to understand than MECKEL's, although he corrects MECKEL's mistake with regard to the corpus callosum.

"My doubts as to the great development of the corpus callosum of the *Ornithorhynchus* were further justified by the indication of its nearer approach to the Oviparous type afforded by the simple bipartite condition of the tubercles called 'quadrigemina.' Well preserved specimens of *Ornithorhynchus* presented to me by Mr. THOMAS BELL, Surgeon, R.N., in 1838, have enabled me to determine this question. There is neither corpus callosum nor septum lucidum in the *Ornithorhynchus*.

"The part described by MECKEL as the corpus callosum corresponds with the fornix and hippocampal commissure, as it exists in the Marsupialia, excepting that the essential function of the fornix, as a longitudinal commissure, uniting the hippocampus major with the olfactory lobe of the same hemisphere, is more exclusively maintained in the *Ornithorhynchus*, in consequence of the smaller size of the transverse band of fibres uniting the opposite hippocampi, and representing the first rudiment of the corpus callosum, as it appears in the development of the placental embryo. The thin internal and superior parietes of one lateral ventricle are wholly unconnected with those of the opposite ventricle."

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[*] MECKEL, 'Ornithorhynchi paradoxi, Descriptio Anatomica,' Leipsic, 1826.

[†] *Loc. cit.* p. 33.

[‡] TODD's 'Encyclopædia of Anatomy and Physiology,' pp. 382 383.

"The part described by MECKEL as the corpus callosum corresponds with the fornix and hippocampal commissure." This is not the case; it corresponds with the projection of the fascia dentata. "The essential function of the fornix, as a longitudinal commissure, uniting the hippocampus major with the olfactory lobe of the same hemisphere, is more exclusively maintained in the *Ornithorhynchus,* in consequence of the smaller size of the transverse band of fibres uniting the opposite hippocampi and representing the first rudiment of the corpus callosum, as it appears in the development of the placental embryo." It would appear from this to be clear that what OWEN regarded as the "longitudinal commissure," is the ridge on the mesial surface made by the fascia dentata, and not a commissure at all. It cannot well be the commissure which I have lettered as *D.F.*, since this runs transversely. Again, which is the transverse band of small size uniting the opposite hippocampi, and representing the first rudiment of the corpus callosum? OWEN has said above that there is no corpus callosum. The transverse commissure (MECKEL's septum pellucidum) is not a small band by any means, although smaller than the anterior commissure. OWEN could not so have described the structure which was figured in MECKEL's plate.

Either description is to me an inscrutable mystery. I cannot understand how MECKEL could have mistaken this thick round commissure for the septum pellucidum, or how OWEN could either have overlooked it altogether or else have described it as "a small transverse band."

On what ground, too, does OWEN maintain that "the essential function of the fornix, as a longitudinal commissure . . . is maintained" when, as will be shown presently, all such fornix as exists in *Ornithorhynchus* decussates in the middle line, is not united with the olfactory bulb, and may be, for all one can tell to the contrary, not a longitudinal commissure at all, but a series of tracts uniting together corresponding parts on the two sides?

The chief interest of the brain of this animal clearly centres about the question as to whether it does or does not contain a corpus callosum, and, therefore it appears to me desirable to sum up the literature of the subject in connection with this question.

Corpus callosum.—In the 'Philosophical Transactions of the Royal Society' for 1837 (p. 80), OWEN asserted that no corpus callosum or septum pellucidum are to be found in either Monotremes or Marsupials. He figures the brains of a large number of species (*Ornithorhynchus* is not amongst them) as showing a "fornix commissure" or transverse commissure superior to the anterior commissure, which represents, however, he says in one place "besides the fornix, the rudimental commencement of the corpus callosum." The same expression is used in his article "Marsupialia," in 'TODD's Encyclopædia,' 1847, for OWEN was evidently not convinced that the corpus callosum is really absent in these animals, although his whole description implies that this is the crucial distinction between non-placental and placental Mammals; a difference which he accounts for by the curtailment of intra-uterine life :—" I have since derived the most satisfactory confirmation of this coincidence from the repeated dissection of the brains of Marsupials belonging to different genera; and although unable to explain how a brief intra-uterine existence, and the absence of a placental connection between the mother and fœtus can operate (if it be really effective and anything more than a relation of simple co-existence) in arresting the development of the brain, yet it is a coincidence which has not been suspected, and is, in various points of view, perhaps the most interesting of the anatomical peculiarities of the quadrupeds here treated of."

In his article "Monotremata," OWEN refers to the transverse commissure which he figures in the brain of *Echidna* as "the hippocampal commissure," but again he says later on that "the short transverse commissure above mentioned is the sole representative of the corpus callosum and fornix."

Whether or not OWEN asserted that the corpus callosum is totally absent in non-placental Mammals (and I cannot find such a definite statement made about any animal except *Ornithorhynchus*), he was understood to mean this, and he himself quotes with approval a table given by MM. EYDOUX and LAURENT ('Voyage de la Favorite,' p. 166) in which it is thus stated, "Corps calleux; Monodelphes (existe); Didelphes (manque); Ornithodelphes (manque); Oiseaux (manque)." These writers add, "MECKEL a cependant admis dans les figures relatives à l'encéphale de l'*Ornithorhynque* l'existence du corps calleux; mais, en étudiant avec soin l'encéphale de notre *Echidné*, nous nous avons reconnu que les descriptions de M. R. OWEN sont plus exactes que celles de MECKEL, et que les déterminations de l'anatomiste Anglais doivent être adoptées."

FLOWER published in the 'Philosophical Transactions' for 1865 (p. 633, *et seq.*) a series of observations upon the brains of *Echidna* and various Marsupials, with the object of disproving OWEN's teaching with regard to the corpus callosum. He did not study the brain of *Ornithorhynchus*, but in the brain of *Echidna* he says, "is seen the superior transverse commissure, very much reduced in extent, and in which the two portions, upper and lower, observed in the Kangaroo are no longer distinguishable," but he adds, "whatever parts of the placental Mammalian brain are represented by this commissure in the Kangaroo are also represented by it, though in a reduced degree, in *Echidna*."

OWEN recognized that the commissures of the non-placental Mammals are not disposed in the same way as, perhaps are not homologous with, the commissures of placental Mammals. He saw the difficulty but not the way out of it; he relied so far as one can judge from his description upon naked-eye observations and very simple dissections, and did not trust his own conclusions. At one time he quotes with approval, as a summary of his own views, the bald statement that neither Marsupials nor Monotremes possess a corpus callosum; at another time he talks about their having the "rudimental commencement of a corpus callosum," and again at another time he gets over the difficulty by naming the commissure the "commissure of the hippocampus."

FLOWER* gives a most admirable and philosophical summary of the position of the question as it rests upon his observations, but in his conclusion he is, as it appears to me, unfair to OWEN. He may well resent the uncertain language which his predecessor used, but he should not deny him the merit of recognising an essential difference between the brains of placental and non-placental Mammals; and had his own observations been carried out, as they would be if made at the present time, by means of a series of sections, he would, I think, have maintained the justice of OWEN's contention that the upper transverse commissure in non-placental Mammals is not sufficiently described as "corpus callosum"; indeed he would, I think, have allowed that the Monotremes, at any rate, have no corpus callosum at all.

FLOWER's summary is too long to quote *in extenso*, but certain sentences may be extracted without giving a false impression. "The commissure radiates over the whole of the inner wall." "They are part of the great system of transverse fibres which bring the two hemispheres into connection with one another." "They cannot in any sense be confounded with the posterior crura of the fornix." "In all Marsupial and Monotreme animals it lies above the septum ventriculorum and especially above the precommissural fibres of the fornix." "Moreover, passing outwards into the hemispheres, it overarches or forms the roof of the lateral ventricles of the cerebrum." The test of a corpus callosum would appear to be summed up in this last sentence. The commissure which we know as corpus callosum consists of fibres uniting together homologous (and also, as SHERRINGTON has shown, heterologous) parts of the convex surfaces of the hemispheres. In *Ornithorhynchus* the transverse commissure in question does not, as my sections show, surpass the limits of the hippocampus.

With regard to other non-placental Mammals I cannot speak from observation, but FLOWER's picture of the brain of *Echidna* represents a condition almost identical with that of *Ornithorhynchus* and HERRICK's figures of sections of the brain of *Didelphys virginica*† show that in this Marsupial animal the disposition of the commissure is the same as in *Ornithorhynchus.* In certain Monotremes and Marsupials, therefore, the commissure does not fulfil Professor FLOWER's test, and it is open to question whether any animal in which the hippocampus extends the whole length of the brain, above the ventricles, can have a corpus callosum.

The hippocampus is the doubly folded margin of the cortex supported by a rod of white fibres, the fimbria or posterior crus of the fornix. If the hippocampus lies above the corpus callosum the fimbria (or fornix) must also have this situation, a curious reversal of the relation which these parts bear to one another in animals in which the corpus callosum is well developed! This is the only arrangement possible unless, indeed, the fibres from the alveus to the fornix interlace with those of the corpus callosum. In *Ornithorhynchus*, however, appearances are altogether against the existence of callosal fibres; the fibres of the anterior commissure which sweep beneath the corpora striata supply the whole of the convex surface, as well as a part of the mesial surface of the pallium.

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* *Loc. cit.*, p. 648.

† 'Jl. of Comp. Neurology,' vol. 2, p. 1. February, 1892.

Professor FLOWER's pictures of the inner surface of the hemisphere suggest that a more or less horizontal plate of commissural fibres, which constitutes the great corpus callosum of Man and most Mammals, is present in a rudimentary form in *Macropus*, *Phascolomys*, and *Thylacinus* (with which he says that *Phalangista* and *Didelphys* agree), but totally absent in *Echidna*.

I find it quite impossible to gather Professor HERRICK's views with regard to the dorsal commissure in *Didelphys*. Under the heading "Callosum and hippocampal commissure," he says* "it is not necessary to recount the various opinions and discussions of the callosum in the Marsupials. Until OSBORN, most authors had agreed that the callosum is absent, and functionally replaced by the anterior commissure." This is curiously oblivious of FLOWER, who especially opposed OWEN on this question, not to mention LEURET, FOVILLE, MAYER (who described *Didelphys virginiana* in 1842), and PAPPENHEIM, who, speaking about the dorsal transverse commissure in the same animal, says,† "le corps en question est bien un corps calleux . . . Cette commissure n'est donc ni un fornix ni un mélange du fornix avec le corps calleux." HERRICK continues, "Professor OSBORN has done much to place this whole subject in its proper light, and we agree with him in respect to the essential homologies of the dorsal commissural system . . . The motor cortex as such is thrown well cephalad, and the fornicate gyrus is carried forward along the mesial surface, as may be seen from an inspection of the transverse sections of Plate A. Thus it happens that the caudal portion of the dorsal commissural system is much more highly developed than the cephalic or callosal portion. The latter consists of a few fibres which spring from the region about the anterior prolongation of the splenial fissure, if this term may be applied to the fissure which bounds the cephalad continuation of the fornicate gyrus." No description of the tract in question is contained in the paper.

ZUCKERKANDL‡ also describes the brain of *Ornithorhynchus*, although he is careful to state that the brain was badly preserved. He also simply names the decussation of the fornix "der rudimentäre Balken," and, although the "Randbogen" is the structure under discussion, he overlooks the fact that it passes right above his supposed corpus callosum to the front of the hemisphere.

If, as appears to me to be the case, the corpus callosum is totally absent in

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* *Loc. cit.*, p. 7.

† "Notice préliminaire sur l'anatomie du *Sarigue femelle* (*Didelphys virginiana*)," 'Comptes Rendus,' vol. 24, p. 186 (1847).

‡ 'Ueber das Riechcentrum.' Stuttgart, 1887.

Ornithorhynchus, it will be necessary to reconsider the whole question of the homology of the commissures in Vertebrata.

Sir WILLIAM TURNER does not describe the interior of the brain in his paper on *Ornithorhynchus*,* but he mentions the appearance of what he considers (adopting FLOWER'S view) to be the corpus callosum. "The anterior commissure and the rudimentary corpus callosum were seen at the surface of the section, and behind these was the hippocampus. A shallow antero-posterior fissure 6 millims. long was observed on the mesial surface of the pallium in front of and above the divided corpus callosum. It might possibly be the splenial fissure, and the slender band of the pallium between it and the corpus callosum would thus represent a rudimentary callosal convolution." The fissure in question, as seen in sections 5 and 6, is the extremely deep dentary fissure (or fossa, as I prefer to call it). The band of pallium, the fascia dentata. Unaware of the continuation forwards of the hippocampus, TURNER saw no reason for considering the dorsal commissure as anything but corpus callosum.

Method.

The whole animal was hardened in spirit. The skull had been opened, and therefore the spirit had at once reached the brain, which was in fair condition.

The left hemisphere was stained in carmine *en bloc* and then cut into an irregular series of sections. Finding, however, that it presented certain points of extreme interest, I determined to treat the right hemisphere with much greater care. It was therefore placed for a fortnight in a two per cent. solution of bichromate of ammonia, for even a brain which, like this one, has been for years in spirit will yield sections which can be stained by WEIGERT'S method if it is placed in a chrome-salt for a time. The hemisphere was next placed in a solution of carmine-alum for a week, washed in water, and after dehydration by alcohols of increasing strength, embedded in celloidin. When the celloidin had been firmly set by chloroform the brain was very carefully divided into fourteen blocks along the lines marked in the photo-lithograph (Plate 20, fig. 1). Each block was then cut into a series of sections of which a number, varying according to the apparent interest of the region, were mounted and labelled A to D or M or N as the case might be; about 150 sections in all (not including some 120 already prepared from the left hemisphere). A certain number of sections from each block were stained by WEIGERT'S method in order that the arrangement of the fibre-tracts might be determined with certainty.

Figs. 6–10 are diagrammatic, inasmuch as the cortex is not coloured at all, and the fibres are shown as they appear in the nearest section of the series which was stained with hæmatoxylin.

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* 'Jl. of Anat. and Physiol.,' vol. 26, p. 357, April, 1892.

Description of Several Parts of the Brain.

The olfactory bulb is of moderate size, its maximal coronal dimensions being vertically 3 millims., transversely 4 millims. Its length is 3 millims. It is absolutely free from the cerebral hemisphere, the rounded neck of the crus, if such an expression is allowable, being crossed by the large anterior cerebral artery on its way to the outer surface.

The bulb is cupped on the under side, as in *Didelphys virginica* described by HERRICK;* the cupping is not, however, visible from the under surface, for it is occupied by glomeruli which lie in loculi of connective tissue. I do not gather from HERRICK's description or pictures that such an arrangement is found in *Didelphys*, nor am I acquainted with any animal in which it obtains.

The ventricle of the bulb is obliterated.

In minute anatomy the bulb presents no feature of particular interest.

The olfactory crus remains for some distance distinct from the hemisphere. It becomes progressively thinner until just before its attachment it is a flat band 2 millims. wide by ·5 millim. thick. The fibres of the olfactory tract lie on its ventral surface. It is situate remarkably near to the middle line at the spot where it adheres to the under surface of the hemisphere.

External form.—The general form and external appearance of the brain have been described so recently by Sir WILLIAM TURNER† that it is unnecessary for me to repeat a description which is already in the hands of all students. I would merely point out certain respects in which the brain is somewhat remarkable. Although the distinction between the rhinencephalon (using this term in an inclusive sense) and the rest of the hemisphere is deeply marked, the brain is absolutely destitute of convolution in the proper sense of the word. It is almost a pity that the furrow (the ectorhinal fissure) which separates the rhinencephalon from the rest of the hemisphere, is named a "fissure," for its origin is not due to the same mechanical causes as the origin of the fissures proper. Rather does it fall into the same class with the incisura pallii longitudinalis (longitudinal fissure) and incisura pallii transversa (transverse fissure) which are the gaps between the different organs which collectively constitute the brain. It is almost a crime to add another to the terms with which the nervous system is already smothered, but I am inclined to suggest that just as longitudinal and transverse fissures have given way to incisura pallii longitudinalis and incisura pallii transversa, so the ectorhinal (or, in human anatomy, collateral fissure) should give way to "incisura rhinalis."

The so-called "choroidal fissure" is not, of course, a fissure in any sense of the word. I have in another paper‡ suggested that it should be termed "hiatus ventriculi."

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* 'Jl. of Comp. Neurology,' vol. 2, p. 1. February, 1892.

† 'Jl. of Anat. and Physiol.,' vol. 26, p. 357. April, 1892.

‡ "The Hippocampus," see p. 389, *infra*.

Is the dentary fissure a true fissure? The fact that the same terminology is used in this as in other parts of the brain has led, as I think, to fruitless attempts to homologize the several structures which make up the "hippocampus" with other parts of the pallium. The hippocampus is altogether different in constitution from the rest of the pallium, and forms, as was recognized by BROCA and by ZUCKERKANDL, a part of the rhinencephalon. Topographically it belongs to the rhinencephalon. It varies in size with the rest of the rhinencephalon. Its essential constituent, the fascia dentata, is, as I have shown in the paper referred to, absent when the olfactory bulb is absent.

The cerebral cortex is divisible, therefore, into the part which belongs to the rhinencephalon and the part outside it.

If we accept the view that the convolution of the brain is due to mechanical causes, that is to say, to the necessity for disposing of a layer of superficial tissue, the nutrient needs of which forbid its increase in thickness beyond a certain maximum, which is reached in very small brains, and which can only be disposed upon the surface of larger brains in a plicated manner; since, while the contents of a sphere equals πr^3, its superficies equals πr^2 only; it is obvious that the use of the word "fissure" in two distinct senses can only lead to confusion.

The formation of the dentary fissure is clearly not due to the causes just mentioned; indeed, the rhinencephalon is distinguished from the rest of the hemisphere by its slight tendency to convolution, and, therefore, in this case also, the use of the word "fissure" might be dropped with advantage and the term "fossa," *i.e.*, dentary fossa, used instead.

The hemispheres are absolutely destitute of convolution, although the projection upwards of the lateral lobe of the cerebellum causes the formation of a deep pit, which separates the occipital from the back of the temporo-sphenoidal region.

The external surface is deeply channelled by blood-vessels which lie in rounded grooves. The greater number of these vessels are branches of the anterior cerebral artery, which reaches the external surface by passing just above the base of the olfactory bulb, separating its crus from the frontal portion of the hemisphere which lies above it. Immediately on reaching the outer surface it divides into two branches, from which are derived other vessels which, diverging from one another, groove the outer surface of the hemisphere as far as its posterior border. A small branch of the anterior cerebral passes to the outer surface beneath the olfactory bulb.

The middle cerebral artery reaches the outer surface at a spot which may probably be regarded as the situation of the fissure of SYLVIUS, and breaks up into branches which do not supply so extensive an area as the anterior cerebral.

The ventral surface presents, at the front, the olfactory bulb. To the outer side of the bulb lies the optic nerve, and to the outer side of this again the immense fifth nerve. The dura mater constitutes a firm sheath for these structures which could not in my specimen be removed without injuring them.

The mesial surface presents at its upper part the unconvoluted internal surface of the hemisphere, of uniform breadth (5 millims.). It is grooved by five small arteries, which pass to its upper border from the posterior cerebral artery. They incline backwards as they pass towards the upper edge of the hemisphere. Behind the corpus callosum, *i.e.*, for more than half its length, the cerebrum forms a flat cap, which rests upon the optic thalamus, the mid-brain, and the cerebellum.

The brain is remarkable amongst Mammals in the continuation forwards of the hippocampus to its extreme anterior end; and, lastly, if my observations are correct, in the complete absence of corpus callosum.

The Hippocampus.—The margin of the ventricular slit is formed by the rhinencephalon below, the hippocampus above. These two meet in block 11 at the back of the slit.

The hippocampus lies, therefore, entirely above or dorsally to the velum interpositum. The ventricle has no descending horn, but extends in a horizontal plane above the crus and thalamus.

The cortex cerebri is strongly folded upon itself several times. First at the dorsomesial edge of the hemisphere it descends as a broad flat surface which borders the incisura pallii (longitudinal fissure). This surface has a breadth of 5 millims. Then the cortex returns upon itself about the dentary fossa: its pyramids being at once arranged in the single sheet which is characteristic of the subiculum. The subiculum sweeps round into the cap of fascia dentata.

At no part of the hippocampus is there any ridge of longitudinal white fibres such as is characteristic of the fimbria, but from the very commencement of the hippocampus the convex surface of the cortex, which projects into the ventricle, is covered with a sheet of longitudinally running white fibres. It is best to call this indifferently the fimbria or fornix, although it is the homologue of the fimbria and alveus of higher Mammals, and is by no means a "corpus fimbriatum." It represents both pars libra and pars fixa of ZUCKERKANDL. Nor is there from behind forwards a distinction in the tract into fimbria, posterior pillar and body of the fornix.

The arrangement of this tract with regard to the fascia dentata is interesting. As seen in 10*a* it enters with the pyramidal cell-layer into the concavity of the cap of fascia dentata. The fascia dentata is quite devoid of fibres on its surface, but consists, as in other animals, of a layer of very small cells (granules) three or four deep, covered with molecular grey matter of rather greater density than the superficial layer of the cortex in other regions.

In 9 the fornix (or alveus or fimbria) is thicker and slightly folded upon itself on the deep surface of the fascia dentata.

In 8 it is still thicker and sweeps over the whole of the convexity of the subiculum* to form a continuous white lining for the ventricle.

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* Using the term in a sense suggested in my paper on the hippocampus.

In 7G the fibres are beginning to collect on the mesial side of the hippocampus, in the angle between the fascia dentata and the convex surface of the subiculum.

At 7F the fibres of the two sides decussate in the so-called "rudimentary corpus callosum," or "hippocampal commissure."

In front of the decussation certain columns of fibres are seen running longitudinally in the substance of the mesial wall of the hemisphere. Others, a thick sheet, sweep up the inner side of the ventricle. A third group, now detached from the rest, lies in the angle beneath the outer limb of the fascia dentata. Some of the fibres of the last groups are longitudinal, others sweep into the nucleus fasciæ dentatæ.

The fascia dentata is at first (behind) uniformly curved, then folded at two right angles, then at one acute angle, which is sharpest at 6D, where the mesial limb is continued for some distance on the surface of the hemisphere. (See sections 10, 9, 8, 7, 6.)

The fascia dentata in front of the decussation constitutes a narrow convolution which is continued to the front of block 5, as seen in the lithograph and in the sections.

Its extreme anterior end is shown in the figure 5A.

I have found it impossible to judge the nature of the decussation or commissure of the fornix from the sections.

It is very clear that few, if any, of the fibres of this fornix system extend beyond the hippocampus at either end. It shows, at its occipital end, such a thin coat of white matter that it is impossible that any considerable number of fibres pass beyond the limits of the hippocampus into the medullary centre of the occipital lobe.

Throughout its whole extent the sheet of white fibres which covers the subiculum on its convex (outer) surface, *i.e.*, the alveus or white lining of the inner wall of the ventricle, grows thinner and thinner as the angle between the inner and outer walls is approached. The rest of the ventricle is, as will be presently shown, lined with white matter belonging to the system of the anterior commissure, and it is more likely that the white lining of the inner wall is reinforced by fibres from the commissure than that the lining of the outer wall receives fibres from the alveus.

The numbers of fibres crossing in the decussation is so large that we may infer that but few remain throughout their course in one hemisphere only; but I cannot see in the sections any appearances which enable me to decide whether the fibres from the front of one hemisphere pass to the front or to the back of the other.

Immediately in front of, or rather beneath, the decussation the main body of fibres (excluding the precommissural fibres already referred to) turn downwards and curve backwards as the anterior pillars of the fornix which will be described in connection with the corpus mammillare.

The Anterior Commissure is a transverse tract of great size, its cross-section measuring in my specimen 2·5 × 3·25 millims.

It is separated from the decussation of the fornix by the thin internal edge of the corpus striatum. It rests below upon the grey matter which forms the inner wall of the hemisphere, intervening between the rhinencephalon and its mesial surface. It is, therefore, surrounded by grey matter on all sides. Its fibres form a broad thick sheet which invest and support the corpus striatum.

It is first cut in the middle line in 6E, but its anterior edge being concave, the thick flattened column is met with, obliquely cut, in sections farther forward. Indeed it may with propriety be described as having a forceps anterior and forceps posterior, for the fibres into which it spreads out on either side pass to all parts of the hemisphere.

In front of the decussation it is easy to follow the course of its fibres, for they are strictly limited to the region between the corpus striatum and the cortex; they form a thick external capsule for the corpus striatum; above the corpus striatum they constitute, as already said, the white lining of the outer wall of the ventricle, and supply, doubtless mingled with peduncular fibres, all parts of the cortex.

Behind the decussation the fibres are more difficult to follow, for they become involved with the peduncular fibres, but again, by block 9, they appear to have become distinct, for a mass of fibres lies beneath the nucleus lenticularis in the angle between it and the meso-ventral edge of the hemisphere, which seems to be continuous with the forceps posterior of the commissure, and but little affected by the peduncular fibres which lie dorsally to this part of the nucleus lenticularis.

The Grey Matter of the Hemisphere may be classified in three divisions:—

1. The grey matter of the mesial wall, with the nucleus lenticularis and nucleus caudatus.
2. The cortex of the rhinencephalon, with (or including) the hippocampus.
3. The cortex in general or pallium.

As there is no septum pellucidum, and the lateral ventricle extends for some distance in front of the commissures, the inner wall of the hemisphere includes a triangular region, bounded by the hippocampus above, the ventro-mesial edge below and the commissures behind, which is very difficult to homologize with parts of the human brain. Perhaps it is not possible to homologize it, for the smooth surface of the cortex which in the human brain lies in front of the rostrum, the "terrain desert," belongs to the pallium, and constitutes the common starting ground of the gyrus fornicatus and the gyrus geniculatus (ZUCKERKANDL) which latter dies away into the nerve of Lancisi; while the region which lies in front of the commissure in the brain of *Ornithorhynchus* is completely separated from the gyrus fornicatus by the hippocampus. It appears to be the part which, in higher Mammals, atrophies in becoming the septum pellucidum, as well as the anterior perforated substance.

It is composed of grey matter 1·3 to 1·5 millims. thick; more compact on either surface than in its centre, and containing branched cells of the pyramidal type. The cells are rather larger than those which are scattered uniformly throughout the corpus striatum, about 11 μ broad by 15 μ long, with apical, basal, and axis-cylinder processes; but partly because the tissue, although in many places well preserved, is hardly fit for accurate histological work, and partly because the shape of the cells depends upon the plane in which they happen to be cut, I do not propose to draw far-reaching conclusions from apparent differences in minute structure.

More interesting than its minute structure is the fact that this tissue passes over at the ventro-mesial angle of the hemisphere into the corpus striatum, without the possibility of any line of demarcation being drawn between them.

It would appear, therefore, that the grey matter which lies on the inner side of the hemisphere is a part of the same formation as the nucleus caudatus. This reduces the latter very distinctly to the level of a cortical formation, differing morphologically from other parts of the cortex in the absence of a white coat. The grey matter of the corpus striatum lies on the axial side of the rhinencephalon, which in turn lies on the axial side of the pallium.

This grey formation reaches almost as far forwards as the ventricle, but projects in front of the part common to it and the corpus striatum as a rounded boss. Consequently in 4 the curious appearance is presented of a round nucleus of grey matter near the ventral edge of the mesial wall, quite distinct from the oval anterior end of the nucleus caudatus.

The anterior commissure passes, as already said, right through this grey matter, so that we find in 6J the appearance of a nucleus of grey matter between the anterior commissure and the commissure of the fornix.

It is noticeable that as the corpus striatum increases in width so also does the grey matter beneath the anterior commissure; the line which marks the outer boundary of the corpus striatum sweeps, therefore, in an even curve beneath the subcommissural grey matter.

The foramen of MONRO is seen in block 7. It is bounded above by the hippocampus and fornix, beneath by a small portion of this grey matter which rests on the anterior commissure.

It is not easy to define the posterior limits of this grey matter. The anterior commissure is last seen in 7J. By this time, as may be seen in the lithograph, the section passes through the third ventricle, and its mesial wall is the epithelial lining of the ventricle. Still the large-celled grey matter, which is characteristic of and common to both the mesial wall of the hemisphere and the corpus striatum, is continued backwards into the angle between the cerebral crura.

It appears, therefore, that grey matter of uniform structure constitutes the mesial wall of the hemisphere in front of the anterior commissure, the corpus striatum, and the wall of the third ventricle. Such at any rate is the conclusion to be drawn from my sections, but I should be very sorry to assert that it would not be possible in a really well-preserved brain, successfully stained, to recognize as many different formations as are described in human anatomy, although I am inclined to think that anatomical distinctions have been pushed too far. The minute structure of the brain should always be studied simultaneously with its configuration.

Central Grey Masses.—In describing the grey matter of the interior of the cerebrum, I have purposely used the expression corpus striatum, because in its anterior position it is not distinguishable into nucleus caudatus and nucleus lenticularis.

The corpus striatum is first seen towards the back of block 4 on the outer side of the ventricle, very near to, but not quite at, its anterior extremity. Its form in section, at this level, is a long oval placed obliquely. It is pierced by a few large bundles of peduncular fibres. It has a thick tract of longitudinal fibres at its upper end, between it and the epithelium of the ventricle, and it is supported on its outer side by ascending fibres of the anterior commissure.

Its ground substance is dense and stains darkly. Its cells are round, fusiform, or triangular with rounded angles. They measure 12 μ to 14 μ in diameter. They are frequently grouped in twos, threes, or fours.

In 5 the transverse section of the corpus striatum is much larger than in 4. The number of peduncular fibres by which it is traversed, especially at its upper part, is much greater. Although the cells in the grey matter on the mesial wall of the ventricle are somewhat larger than those in the corpus striatum, it appears, as already remarked, impossible to make a distinction between these two formations. The three regions, mesial wall of hemisphere, substantia perforata anterior, and corpus striatum are anatomically indistinguishable.

In 6 the corpus striatum is limited below and on the outer side by the anterior commissure. The number of penduncular fibres has increased greatly and bundles are beginning to divide its upper part into separate nuclei.

In 7 the number of fibres is still further increased so that the grey matter is honeycombed with them, and a portion of the grey matter which lies beneath the ventricular epithelium is continued across the middle line beneath the velum interpositum. This is rather an unexpected arrangement, for in the last sections of block 6, where the anterior commissure is at its maximum development, the ventricular slit reaches right down to the anterior commissure save for a thin sheet of ependyma, and the grey matter of the mesial wall is therefore completely separated from the corpus striatum, but as the vertical height of the anterior commissure is diminished, grey matter again intervenes between the commissure and the ventricle and follows the commissure across the middle line, so that the two corpora striata are in continuity through the medium of a thin sheet of grey matter which invests the anterior commissure. It is but a very thin sheet, for it is soon occupied by the descending fibres of the fornix, which it separates from the back of the anterior commissure, and yet it seems to me of importance as showing that in the absence of a corpus callosum, the grey matter which forms the lateral and anterior walls of the third ventricle passes into the grey matter of the mesial wall of the hemisphere (*i.e.*, of the region which, in brains containing a corpus callosum, becomes the septum pellucidum) and also into the grey matter of the corpora striata.

7r shows the round anterior end of the optic thalamus with fibres on the outer side separating it from the nucleus caudatus; the velum interpositum resting on its upper surface and descending fibres of the fornix thrusting it aside from the ventricular cavity. This will be described immediately.

The nucleus caudatus is hardly as yet separated from the nucleus lenticularis, but a very large number of bundles of fibres, some large, some small, are cut transversely. They clearly enter the corpus striatum from behind, and are, for the most part, destined for its substance, but in all sections a certain number may be seen emerging from the outer surface of the nucleus and joining the system of fibres belonging to the anterior commissure. It is impossible to follow the course of such bundles of fibres in a series of transverse sections, but there cannot, I think, be much doubt that (1) the majority of the peduncular fibres which enter the corpus striatum from behind are lost in its substance; (2) a number of bundles traverse the corpus striatum to reach the cortex; (3) while it is impossible to say whether all the bundles of fibres which are seen partly within and partly without this body are passing directly from the peduncle to the cortex, few if any are entering from its cortical surface to lose themselves in its substance.

A remarkable difference in structure between the ventricular and extra-ventricular portions of the corpus striatum has now become established. Towards its convex surface, its cells are, as in its anterior part, both large and numerous. The ventricular portion, on the other hand, shows a denser more deeply staining ground substance, but few cells, and these are not so large as in the outer portion.

7L. The peduncular fibres may now be said to form an internal capsule. The grey commissure is seen bridging across between the thalami.

8A. The nucleus lenticularis, as a thin capsule of grey matter, sweeps round the outside of the internal capsule and above the portion of the anterior commissure exposed in this section, into the cortex of the pyriform lobe. It is traversed, or partially traversed by many bundles of fibres; those which separate it from the nucleus caudatus differing from those which traverse it elsewhere merely in being an association of bundles larger than the rest. On its basal side the bundles are so numerous as to leave but a network of grey matter amongst them. The nucleus caudatus is contracted into an oval column.

9H. An inner nucleus fills the concavity of the shell of the nucleus lenticularis. It occupies, with regard to the latter, the relation of nucleus ruber to putamen. It seems, however, to be split off from the optic thalamus rather than from the corpus striatum, and, although its cells are not so large as those in the rest of the thalamus, they are nevertheless larger than those of the nucleus lenticularis.

10. The putamen is so thin as almost to resemble a claustrum. It is, however, quite distinct in structure from the large nucleus ruber. A few large cells lie on its concave surface. Its lower thicker border has withdrawn from the cortex of the pyriform lobe.

11G. The nucleus ruber has almost disappeared, but the putamen is still distinct.

The tail of the nucleus caudatus is thicker and inclines towards the temporal cortex.

12. The putamen and tail of the nucleus caudatus, reunited, form a capsule for the central white core of the occipital lobe. It is last seen in 12D.

I am unwilling to draw wide conclusions from the study of a single brain, and shall hope to compare with the brain of Ornithorhynchus brains of Marsupials and Rodents, both adult and embryonic; nevertheless, I can hardly leave the basal grey matter of the hemisphere without pointing out that the appearances presented by a series of sections carried through this region strongly suggest its formation by reduplication in front of the peduncular fibres.

Nucleus caudatus and putamen form a common structure which is continuous with the wall of the hemisphere both in front of and behind the cerebral crus, and appears to be a portion of the wall of the hemisphere which has been thrust outwards (or pitted in) by the crus and optic thalamus.

In minute structure the nucleus ruber resembles the thalamus rather than the corpus striatum.

Cortex.—The brain is, as already remarked, totally destitute of convolution. Save for the grooves made by blood-vessels, and for the bulging of the hemisphere into occipital and temporo-sphenoidal lobes, the cortex forms a uniformly curved case for the white matter and central grey masses. It is, relatively to the size of the brain, very thick, measuring in the spirit-hardened brain at its thinnest part, *i.e.*, on the upper surface of the hemisphere near its internal border, 1·3 mm., at its thickest part, *i.e.*, near the meeting place of the external and basal surface, 3·5 mm., the maximum diameter of the hemisphere being 15 mm.

In minute structure it is extremely uniform, presenting neither marked stratification of the elements of which it is composed at any given spot nor notable differences in structure in different regions, and yet it is easy to see that, both in their relative number and in their arrangement, the elements vary in disposition in different regions.

The "pyramids" are very irregular in form, being as often triangular, stellate, or fusiform as distinctly pyramidal in section. Very frequently the process which would be regarded as apical, were the orientation of the section not known, is directed centrally not peripherally.

Large pyramids are undoubtedly most numerous in the anterior and dorsal part of the cortex, *i.e.*, in blocks 5, 6, 7, dorsal to the corpus striatum.

Only in the cortex of the rhinencephalon, and in certain parts of the inferior and external surface of the hemisphere, are the small pyramids collected into so distinct a layer as in the brain of most Mammals.

The superficial stratum moleculare has a uniform thickness of about 30 μ; it is almost destitute of cells.

The small pyramids commence rather abruptly beneath the stratum moleculare and give way with every transition in size into large pyramids, the maximum diameters of which are about 22 μ and 12 μ; in the occipital region some of the pyramids have a transverse diameter of as much as 17 μ.

Granules are scattered uniformly throughout the layer of pyramidal cells, and nowhere collected in a separate stratum. They are more numerous in the basal and posterior region of the cortex than in the dorsal and anterior region.

Fusiform cells are seen in the deepest stratum of the cortex, but it is only in certain places that they can be said to form a layer.

Perhaps it is justifiable to say, although our standard is uncertain, that the cortex is simple in minute structure.

Optic Thalamus.—This mass of grey matter, although a part of the primary forebrain and not of the cerebral hemisphere, is conveniently included in a description of the latter. It appears first in 7I as a round darkly staining mass supported and enveloped by fibres which enter its substance in thin bundles. The head of the thalamus is in this section separated from the ventricular epithelium by descending fibres (anterior pillars) of the fornix.

7K. The descending fibres of the fornix have divided into two almost equal groups; the one of which runs as a thick bundle along the upper surface of the thalamus, the other descends to the large corpus mammillare. The corpus mammillare depends from the floor of the ventricle as a thick round tubercle of grey matter. Between the two bundles, the thalamus reaches the middle line, in the grey commissure.

7L. An immense number of bundles enter the thalamus from its under and outer sides. Large when they first enter, they rapidly diminish in size. Beneath the thalamus they interlace with fibres of the internal capsule and curve both inwards and outwards, in a manner which renders it unwise for me to make assertions with regard to their destination.

8A. The thalamus has increased greatly in size and its outer part, which is traversed by many bundles of fibres, differs from its inner portion in structure.

The middle, soft, or grey commissure occupies the whole of block 8 and a large part of block 7. The bridge is not by any means, however, limited to grey matter, for a distinct and considerable tract of fibres crosses in its posterior and lower portion. They spread out in all directions after passing the middle line.

The portion of the thalamus which enters into the formation of the wall of the ventricle is continuous with the corpus mammillare and projects between the crura cerebri. It causes the crura to be thrown far outwards so that in 8C, for example, the fibres of the crus lie on the outer side of the thalamus rather than beneath it.

The thalamus is still seen in the anterior sections from block 10 in which the aqueduct of Sylvius and the grey matter around it also appear, but its outer margin is ill defined.

Comparatively simple although the structure of the brain of this lowest of Mammals is, it is nevertheless vastly too intricate to allow of the analysis of its fibre-tracts by means of series of coronal sections only. I have, therefore, confined myself in my description to its more striking features.

In the hope that I may soon receive from Australia some brains of *Ornithorhynchus* thoroughly well hardened in a chrome-salt by an expert collector, I have abstained from describing in this paper many things which my sections show in a fairly satisfactory and unmistakable manner.

Corpus Mammillare.—This body is large and well-defined, and great interest attaches to its structure in this animal on account of the great size of the fornix, for it would seem to offer an opportunity of settling the vexed question of the relation, to the corpus mammillare and to one another, of the descending pillar of the fornix and the bundle of Vicq d'Azyr.

From the decussation of the fornix a certain number of fibres enter the mesial wall of the hemisphere in front of the anterior commissure, but by far the greater number curve backwards and downwards on either side in the wall of the ventricle as the anterior pillars of the fornix, which almost rest upon the back of the anterior commissure.

In 7I the whole column appears to be descending, but in 7J it is seen that only part, about one-half, of the fibres descend, the rest begin to ascend again, resting on the upper surface of the optic thalamus. The descending fibres sweep down at some little distance from the ventricular epithelium towards the corpus mammillare, or rather towards the deep prolongation of the floor of the ventricle which occupies the situation of this structure between the crura cerebri. A small number of large cells, with their long axes placed vertically, lie amongst these fibres just above their entrance into the back and outer side of the corpus mammillare.

The bundle which passes backwards beneath the foramen of Monro and then skirts along the dorso-mesial edge of the thalamus in the situation of the tænia thalami needs investigation.

Had I stained all the sections on one side of the brain by WEIGERT's method it would doubtless have been possible to follow the course of these several bundles of fibres; as it is I can merely point out that the study of the brain of *Ornithorhynchus* will probably enable us to determine the course of several at present ambiguous tracts.

Minute Structure of the Thalamus.—The appearance presented by this tissue in my sections depends upon its deficient preparation; but while I am unwilling to enter into a detailed description of the microscopic appearance of a tissue which has not been prepared especially for this purpose, I am bound to say that this brain is sufficiently well hardened to show all the more important features of its structure, and that the different parts of the brain may well be compared with one another.

The anterior tubercle of the thalamus consists of a dense, darkly-staining matrix, containing large round cells. These cells differ, however, in a marked way from the cells of the corpus striatum and of the cortex, for instead of staining darkly and exhibiting well-defined angular bodies, they belong to the type of soft cells, the bodies of which are seldom seen, since they break down in the hardening reagents, leaving behind nothing but clear round vesicular nuclei lying in round spaces.

It is not uniform in structure, however. Its posterior portion which spreads far outwards into the internal capsule, by the bundles of which it is traversed, contains cells which are much larger and more definite in form than any to be found in its anterior portion or in the corpus striatum. The largest of these are found on its under side where they form an almost distinct group, homologous probably with one of the subthalamic nuclei. They measure as much as 30 μ by 14 μ. Their long axes are placed horizontally, and they appear to be in connection with the white fibres which cross the middle line on the under side of the commissura mollis. Athough the largest of the cells form an ill-defined group by themselves, others almost as large are found throughout this region, and extend across the middle line in the commissura mollis.

[This paper contains little more than a series of detached observations, which are published with some reluctance. Although I had been familiar with the main facts in the cerebral organization of *Ornithorhynchus* for some years, I had postponed their publication in the hope of obtaining a supply of well-preserved specimens, from which it would be possible to construct a complete monograph. The interest which attaches, however, to the description of the corpus callosum as a chapter in the history of science, and the peculiar features in the disposition of the rhinencephalon, which may serve to throw light upon the relation to one another of the two portions of the cerebral hemisphere, seemed to justify a preliminary communication.

Since this paper was written, DR. JOHNSON SYMINGTON has published observations which confirm my conclusion that the corpus callosum is absent in *Ornithorhynchus*. DR. SYMINGTON, indeed, extends this statement so that it includes all non-placental Mammals:—"It appears to me, therefore, that the cerebral commissures in the Monotremata and Marsupialia present several characters by which they can be distinguished from those of the placental Mammals, viz., (1) the anterior commissure is as large, and generally much larger, than any other transverse commissure of the cerebrum, and it unites the whole of the cortex of the two hemispheres, except the gyri dentati and hippocampi majores; (2) they have no true corpus callosum; and (3) the superior transverse commissure is simply a commissure for the gyri dentati and hippocampi majores."*—A. H., June, 1893.]

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* JOHNSON SYMINGTON. "The Cerebral Commissures in the Marsupialia and Monotremata." 'J. of Anat. and Physiol.,' vol. 27, p. 69, October, 1892.

DESCRIPTION OF PLATES.

PLATE 20.

Fig. 1.—Photo-lithograph of the right half of the brain of *Ornithorhynchus* from the mesial aspect. *Magnified 2 diameters.*

The lines indicate the divisions between the blocks into which the brain was cut. A series of sections was taken from each block. The dura mater was left on the basal aspect of the brain.

Section 4E.—Carried through the extreme anterior end of the lateral ventricle, shows the junction of the flat olfactory crus with the under side of the hemisphere.

Section $4E_2$ exhibits the commencement of the nucleus caudatus on the outer wall of the ventricle. A distinct nucleus of grey matter is also seen at the ventro-mesial angle of the section; the fibres of the olfactory crus form a narrow area to the outer side of this nucleus.

Section 5A.—The anterior end of the hippocampus. The fascia dentata lies almost at right angles to the plane of the large pyramids of the subiculum. Fibres from the front of the commissure of the fornix are descending in the ventricular wall.

Section 6D.—Diagrammatic view of a section in front of the commissure of the fornix and the anterior commissure. The appearance of the fibres as stained with WEIGERT's hæmatoxylin, has been added to a drawing made from a carmine preparation. The cortex is curving over into its scabbard of fascia dentata. The fibres of the fornix system constitute a capsule for the hippocampus, to which they are limited. The lateral, superior, and part of the mesial cortex is supplied by fibres of the anterior commissure.

Section 6J passes through the anterior edge of the commissure of the fornix, and cuts the anterior commissure. It shows the continuity of the grey matter of the mesial wall above and below the anterior commissure with the nucleus caudatus. On the ventral side of the section is seen the rhinencephalon, bounded both on its mesial and lateral aspects by fissures, which leave but a narrow sheet of fibres as a connection between it and the rest of the hemisphere.

PLATE 21.

Section 5B_2, through the extreme anterior end of the hippocampus, shows the relation of the fibres of the fornix-commissure to the mesial wall, and the descent of its precommissural fibres. The tract of cortex to which the fibres of the olfactory crus are applied is beginning to be separated from the general cortex by mesial and lateral fissures.

Section 7F cuts the commissure of the fornix.

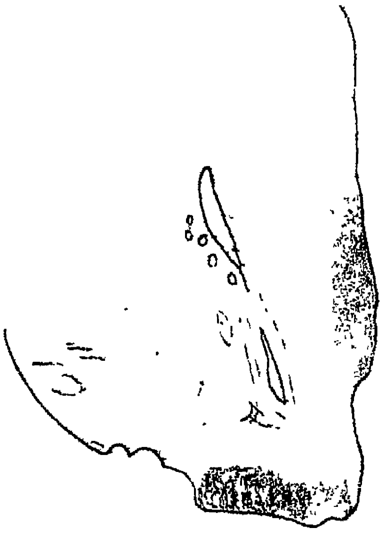
Section 7G is carried just behind this commissure.

Sections 8, 9, 10G show the way in which the fornix dies away upon the surface of the hippocampus behind its commissure.

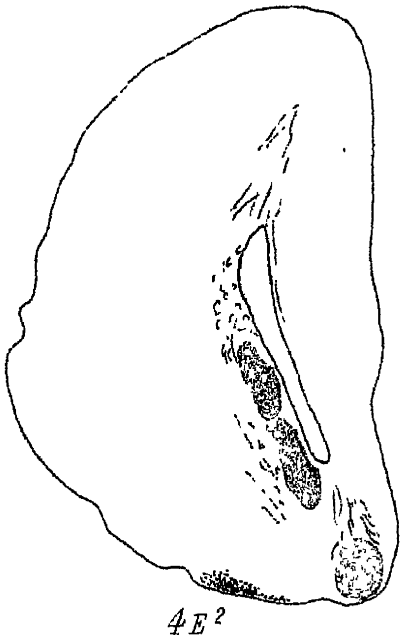
PLATE 22.

Sections 7E, 7J, 7K_2, 8C, 9E, from preparations stained after WEIGERT'S hæmatoxylin-method.

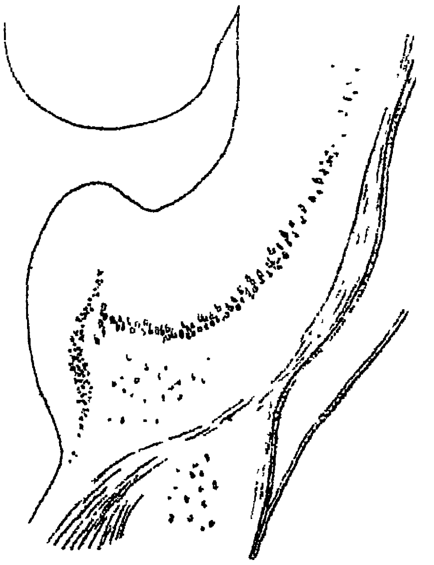
F.	Fornix.
D.F.	Decussation or commissure of the fornix.
D.P.F.	Descending pillars of the fornix.
S.C.B.	Supra-commissural bundle (tænia thalami).
A.C.	Anterior commissure.
W.C.	White fibres in the commissura mollis.
O.T.	Optic tract.
C.O.	Optic chiasm.
P.L.	Pyriform lobe (rhinencephalon).
C.S.	Corpus striatum.
N.C.	Nucleus caudatus.
P.	Putamen.



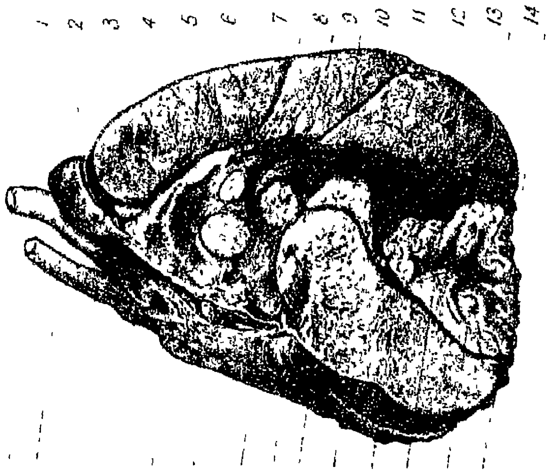
4E



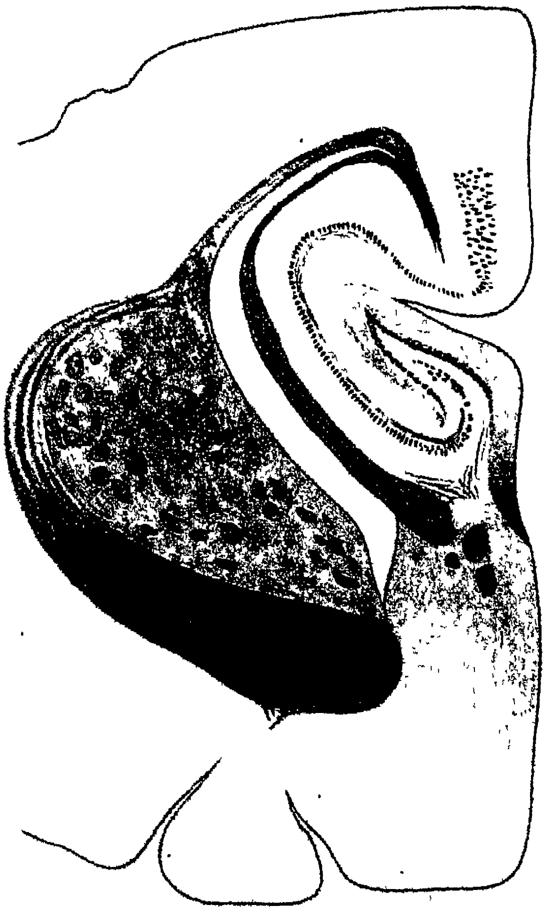
4E²



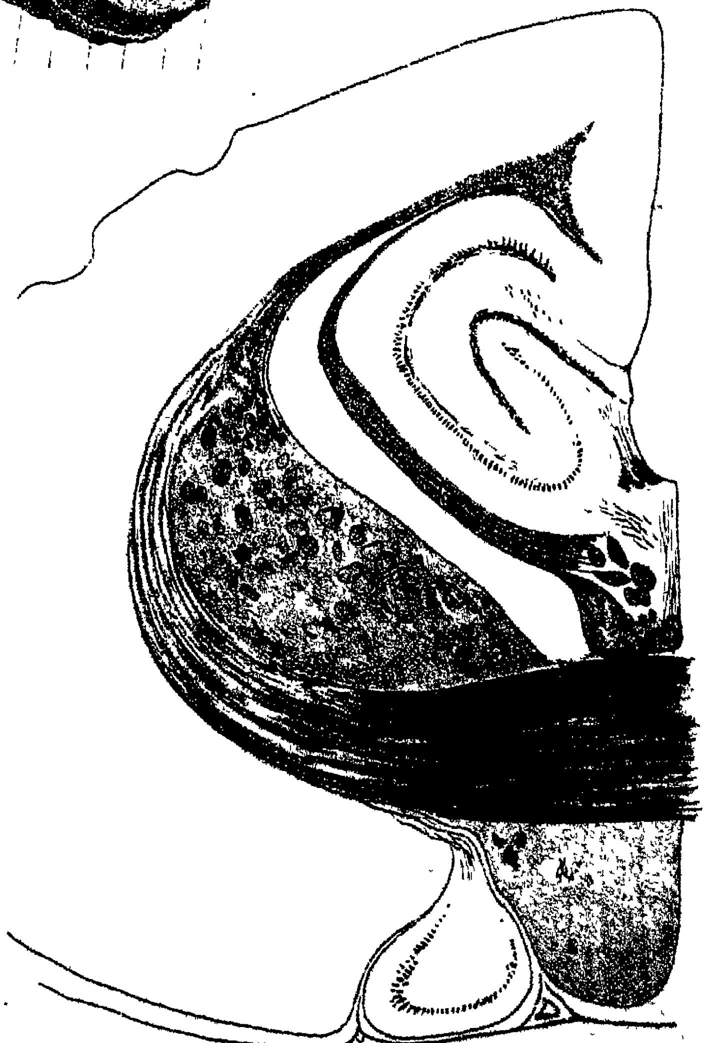
5A



1.



6D



6J

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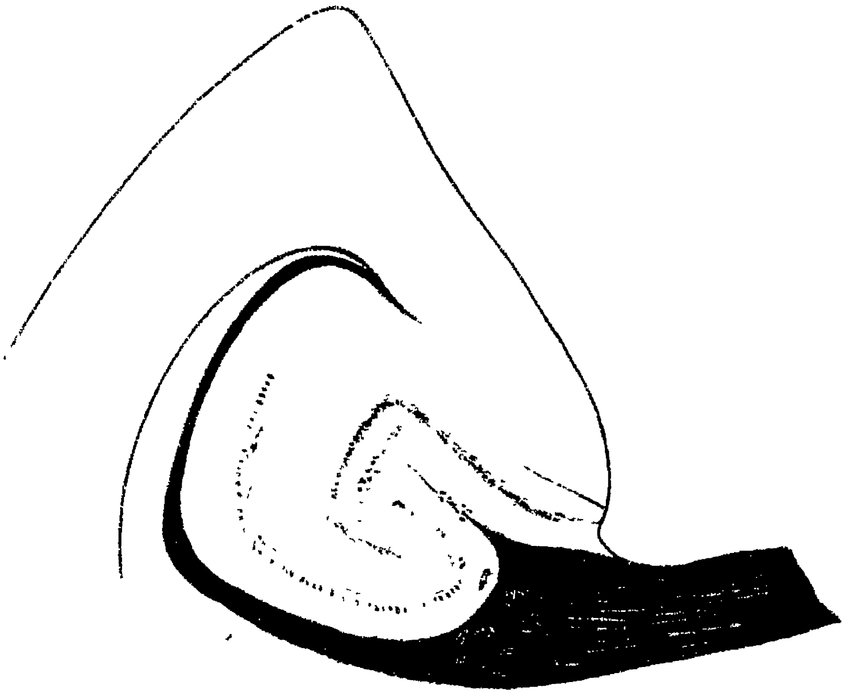
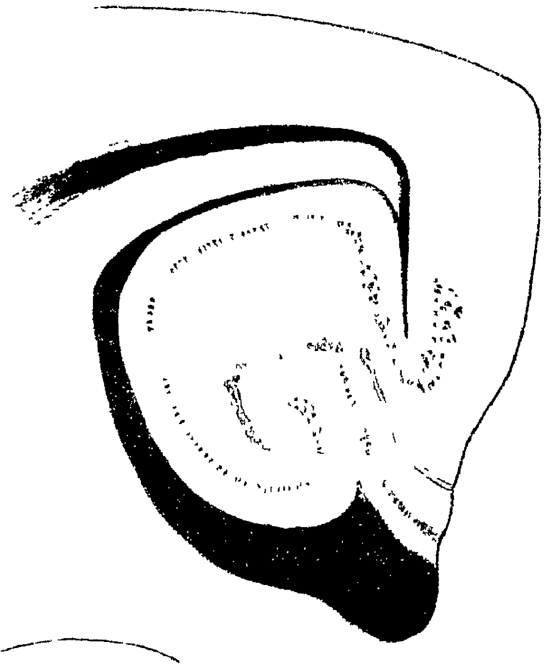
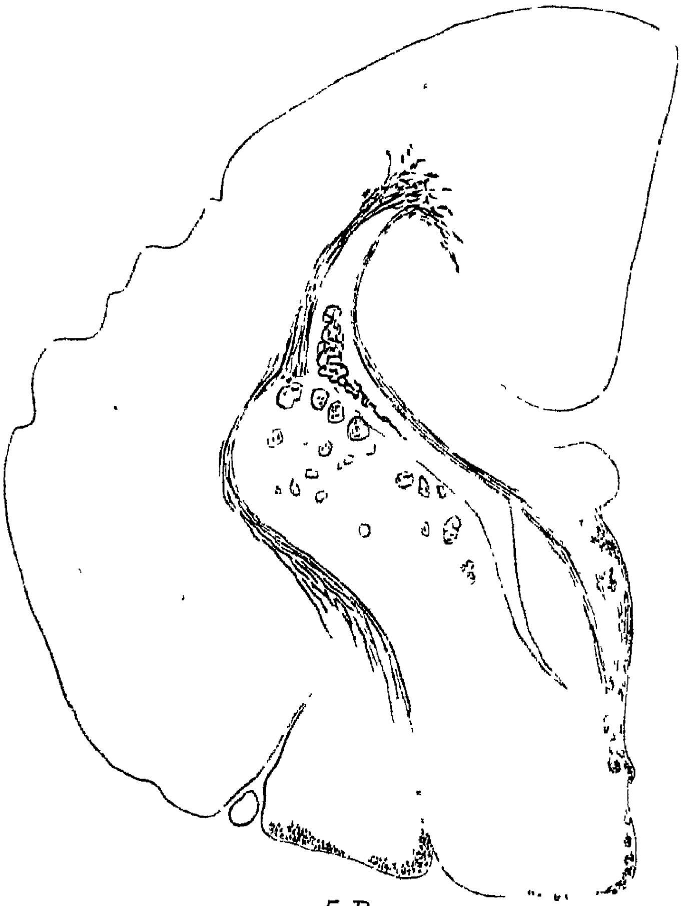


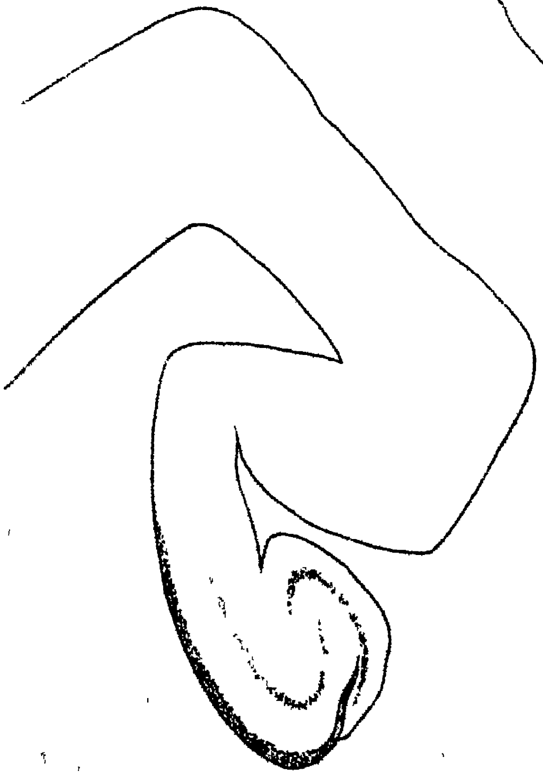
7 F.



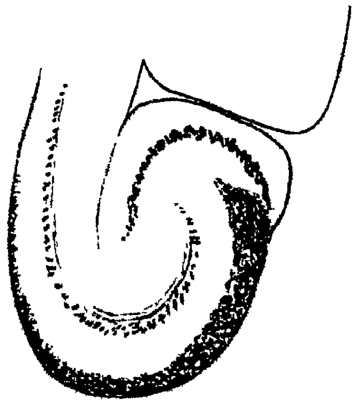
7 G.



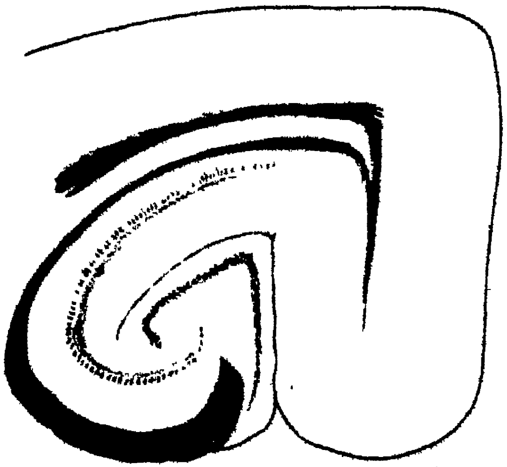
5 B 2.



10 G.



9.



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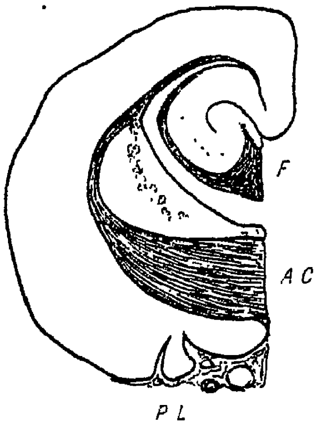

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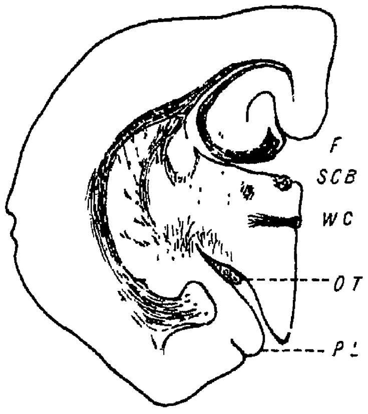

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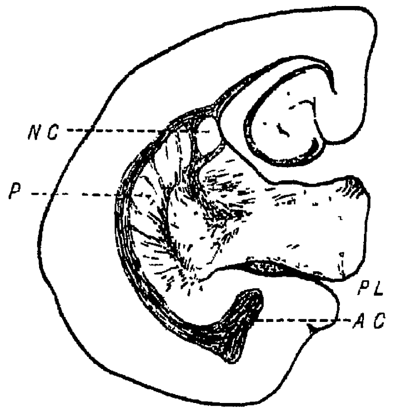

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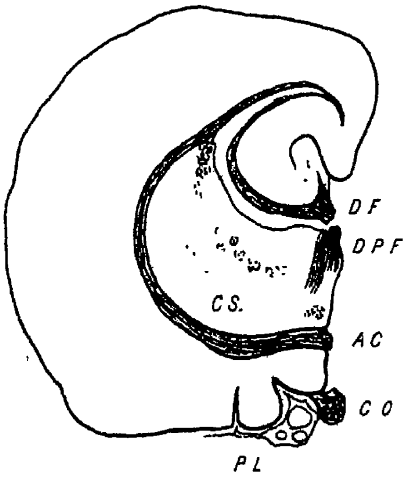

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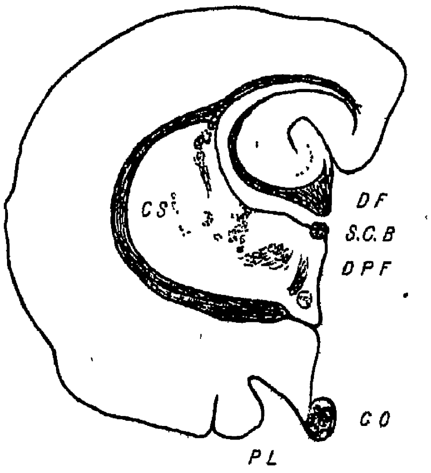

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VI. *The Hippocampus.*

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Communicated by Professor Alexander Macalister, *M.D., F.R.S.*

Received May 4, 1892,—Read June 2, 1892.

[Plates 23–25.]

Nomenclature.

It is only within quite recent times that anatomists have realized that the comparisons with which they help out their descriptions of parts of the brain are likely to become fixed as the names of the parts. Even in the beginning of this century—indeed the custom has not altogether ceased even yet—they quoted the illustrations used by their predecessors, to replace them at once by new ones, if any, more apposite, occurred to them, without recognising the risk of confusion likely to arise from the multiplicity of names. There is a curious alternation between the use of the simile as an unalterable symbol and as an aid to description. In other words, we strike in quite recent anatomical strata upon stages in word-formation which are deep down in the history of other sciences.

Galen converted illustrations into cognomens for most of the bones, muscles, and other parts of the body, but the anatomists of the 17th and 18th centuries, when writing of the parts of the brain, considered it as immaterial whether or not they used the same symbols or illustrations as their predecessors; they did not regard its terminology as in any degree fixed, and if a new illustration occurred to them which conveyed a better idea of the form of the part than any as yet current, by all means let posterity make use of it!

Thus we find the region about to be described compared to and named as:—Hippocampus, pes hippocampi, bombyx, appendix bombycinus, vermis bombycinus, baco, processus cerebri lateralis, protuberantia cylindroides, cornu arietis, cornu Ammonis; with innumerable variations in the translation of the foregoing terms into French and German:—hippocampe, corne de bélier, corne d'Ammon, Ammonshorn, Widderhorn, Reil'sche Kolbe, &c.

Nor does the confusion end with the selection of a suitable name. The limitation of the part is as uncertain as its nomenclature. Thus, we find the term "pes hippocampi" applied to the swelling within the descending horn of the lateral ventricle;

to the anterior part of this swelling only, with a loose use of the term "hippocampus" for the swelling as a whole; to the swelling *plus* its fimbria, or *plus* its fimbria and the fascia dentata. Indeed, the use of the term as including all these parts appears to be the older: "pars longior cum proxime cruribus fornicis interjecta, cerebri medulla unitur et cum hippocampo comparata in arcum flectitur."[*]

If out of all the terms in use it were open to us to choose the most apposite, "cornu Ammonis" would be the one upon which our selection would fall. This is the term preferred by Schwalbe,[†] although he seems to me to overlook its descriptive value when he limits it to the "halbmondförmig gekrümmter Wulst von ungefähr 50 millims. Bogenlänge, der vom Balkenwulst an zunächst dem vorderen concaven Rande des Trigonum ventriculi lateralis folgt." The peculiar applicability of the term is not appreciated until the brain is dissected away from above, as often happens, almost by accident, when the brain is semi-putrid, and the two gently curling horns exposed in their whole extent. Exclude the fimbriæ, and the illustration is almost pointless!

I should have selected the expression "cornu Ammonis" for application to the whole region had it appeared justifiable to neglect the classical expression "hippocampus or pes hippocampi"; but it appears that this name was already fixed before its likeness to the horns of the Horned-Jupiter occurred to any anatomist.

The part was first described and named by Arantius[‡] "hippocampi vel bombycini vermis ventriculos appellare libuit."

Diemerbroek, writing in 1632, attributes the name "pes hippocampi" to Hippocrates, but I cannot find the reference, and the anatomists of the 17th and 18th centuries who were likely to be deeply read in Hippocrates are unanimous in assigning it to Arantius.

Vieussens, in his 'Neurographia Universalis,' written in 1585, just before the date of Arantius' work, while giving a somewhat elaborate description of the part, uses no name: "crura posteriores corporis callosi seu veri fornicis columnas nuncupamus . . . . cruribus intermediam fimbriatam veri fornicis appendicem nominamus."

Caspar Bauhin,[§] in 1621, says: ". . . parte posteriore fulcra duo obtinet, quæ posterius deorsum reflexa velut novas cavitates constituere videntur, quas ventriculos hippocampi, ab animalis forma, posteriores denominare solent. *Pedes hippocampi nominantur ab Arantio.*"

Ridley,[‖] in 1695: "Hippocampi Arantii or bombyces."

J. and C. Wenzel[¶] explain: "Processus cerebri lateralis, vulgo hippocampus ab Arantio qui processum istum primus descripsit."

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[*] Haller, 'Elementa physiologiæ,' lib. 10, sect. 1, 1762.

[†] Schwalbe, 'Lehrbuch der Neurologie,' p. 513.

[‡] 'Anatomicarum Observationes,' cap. 3, 1587.

[§] 'Theatrum Anatomicum,' lib. 3, cap. 13.

[‖] 'Anatomy of the Brain.'

[¶] 'De penitiori structura cerebri hominis et brutorum.' Tübingen, 1812.

It seems to be clear, therefore, that this region was first described by ARANTIUS, and that his comparison to the "pes equuli marini" was adopted as its name.

I have been unable to trace the origin of the term "cornu Ammonis."

MORAND[*] terms the region "cornes de bélier"; but, he remarks, "qu'une partie de l'embarras qui se trouve à concilier les anatomistes, vient de ce qu'ils ont donné indifféremment le nom de cornes de bélier aux ventricules et aux parties qui y sont contenues. Ce sont celles-ci qui sont vraiment les cornes de bélier ou l'hippocampus suivant ARANTIUS." The three cornua of the lateral ventricle (first called *lateral* ventricle by MORAND) were named some time later by VICQ D'AZYR; the confusion did not arise, therefore, from the application of the term "corne de bélier" to the descending horn.

GUNZ[†] uses the term "cornu arietis." "Quæ cornu in modum flexæ sunt, atque rotundulæ, totæque in illo pariete exstant, hippocampi, vel arietis cornua nominantur"; but the first use of the term "cornu Ammonis" which I have been able to trace is in a series of papers "On the Human Brain," laid before the French Academy by VICQ D'AZYR, in 1781. In obs. ix. (p. 518) he treats of "Les cornes d'Ammon ou hippocampes," and says that "une circonvolution recourbée en manière de crochet désigne leur situation et leur forme." From his description it would be difficult to gather his view as to their external boundary, but his figures make it quite clear that the cornu Ammonis, as he understood it, included the floor of the descending horn as well as the fascia dentata. The latter he terms "la portion crénelée ou bord dentelé de la corne d'Ammon." In his 'Vocabulaire,' VICQ D'AZYR defines: "Hippocampi, pedes hippocampi, cornua Ammonis; les protubérances médullaires recourbées qui sont situées dans la partie postérieure et inférieure des ventricules lateraux." He adds, "je distingue deux espèces d'hippocampes. Les grands . . . et les petits ou ergots dit de MORAND."

Perhaps a more thorough search through the literature of the period preceding the French revolution would reveal the origin of the term, or it may be that VICQ D'AZYR transformed "corne de bélier" into "corne d'Ammon" without thinking the change of name worth noticing. The quotation from HALLER, which is given above, is important in this connection, for HALLER, although extremely careful to give synonyms and references, says nothing about cornu Ammonis.

Vulgo "hippocampus" appears to be the established term. The "pes" may be omitted, for it has no meaning when applied to the hippocampus minor, and can hardly be retained without rendering the expression cumbrous when the subiculum (pedis) hippocampi, gyrus (pedis) hippocampi, &c. are referred to.

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[*] 'Histoire de l'Académie,' 1744, p. 6.

[†] 'Prolusio observationes anatomicas de cerebro continens altera.' Leipsic, 1750.

Interpretation of the Hippocampus.

By all anatomists with whose works I am acquainted the whole of the hippocampus is regarded as a part of the cortex. "On doit regarder la corne d'Ammon ou grand hippocampe comme une circonvolution cérébrale d'une forme particulière," says Vicq d'Azyr; containing, that is to say, the same elements as are found in other parts of the cortex (although they are differently arranged) and no elements which are not found elsewhere. The hippocampus is always spoken of as a composite of convolutions, the only difference of opinion being as to the number of convolutions represented. Since the time when Zuckerkandl[*] pointed out that the striæ longitudinales lateralis et medialis (the stria obtecta and nervus Lancisii, as they are usually called) belong to the mesial surface of the brain, being developed from the dorsal portion of the outer arcuate convolution of Arnold, while the ventral portion of the same convolution becomes the fascia dentata, the problem has altered somewhat in form, but it remains essentially the same as in the days of Vicq d'Azyr. It is taken for granted that the arcuate convolutions of Arnold are portions of the mantle, homologous with those other parts which develop into the convolutions of the general surface of the adult brain.

In a recent memoir, Honegger[†] has most laboriously analyzed the literature of this subject, and it would therefore be unnecessary for me to go through it a second time, even if I thought that it would throw any light upon the subject of this paper. The sum of this investigation is that Zuckerkandl traces the stria lateralis (seu obtecta) into the fascia dentata; Honegger traces the stria medialis into the fascia dentata, while the lateral stria passes, he says, into the superficial layer of the gyrus hippocampi. Ganser[‡] denies that the fascia dentata is continued in any way on to the dorsal surface of the corpus callosum. Giacomini's views will be discussed later.

It is doubtless of great importance that these stages in the development of the margin of the porta should be traced with exactitude, but before the facts can be applied to the determination of the homology of the hippocampus certain antecedent questions must be answered, and still earlier stages in the development of Arnold's convolutions must be worked out in order that we may be placed in a position to judge whether they are in any respects comparable to the convolutions of the general surface of the great brain. In particular we need to know the relation which Arnold's convolutions bear to the olfactory crus and bulb. If the external stria of the olfactory tract passed into any part of the hippocampus we should have data from which to speculate; but this is not the case. Although I have cut a great number of sections in all possible planes from the temporal pole of brains of various animals, I am unable to trace the ultimate connection of the external stria, but I can with confidence assert that it does not go, as HERRICK* conjectures, into the lamina nuclearis and superficial bundle of the fascia dentata. Until, therefore, something more is known as to the morphogeny and histogeny of ARNOLD'S convolutions, no light will be thrown upon the morphology of the hippocampus by the study of the relations of the several portions of these convolutions in the adult brain.

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[*] Zuckerkandl, 'Das Riechcentrum.' Stuttgart, 1887.

[†] Honegger, "Vergleichend-anatomische Untersuchungen über den Fornix und die zu ihm in Beziehung gebrachten Gebilde im Gehirn des Menschen und der Säugethiere." 'Recueil Zool. Suisse,' vol. 5, Nos. 2 and 3, pp. 201–435. December, 1890.

[‡] Ganser, "Gehirn des Maulwurfes." 'Morphol. Jahrb.,' vol. 7, 1882, pp. 591–725.

Whatever its origin, all anatomists who have written on the subject up to the present time agree in regarding the fascia dentata as a convolution, or as a part of a convolution, and as this is not the view of the writer of this paper, little would be gained by giving an account of the attempts which have been made to homologize it with other convolutions. Such theories as have been published may be classified in three groups:—(*a*) Fascia dentata *plus* nucleus fasciæ dentatæ constitute one convolution, the small cells of the stratum granulosum being the small pyramids of the gyrus (subiculum) hippocampi collected together in a separate cluster (HENLE, KRAUSE, MEYNERT, HUGUENIN, SCHWALBE, OBERSTEINER, &c.); (*b*) the fascia dentata is an independent convolution, cells of all layers being represented in its granules (DUVAL); (*c*) it is an independent convolution, but inverted (GOLGI, SALA).

The view last cited† would appear at the first moment to approach most nearly to my own. GOLGI says that the reflected cortex (strato grigio circonvoluto), and the fascia dentata "non devono essere considerati come due zone di un medesimo strato, ma bensi come due distinti circonvoluzioni . . . che la fascia dentata sia una diritta continuazione anzi un' espanzione della lamina grigia circonvoluta." Such embryological investigations as I have yet been able to make, lead me to believe that the inner margin of the wall of the great brain is folded into a pouch, the mesial wall of which folds back to the fimbria, and is carried into the descending horn of the ventricle as the choroid plexus. As said elsewhere, I lay very little stress upon these observations, which require to be checked by a full examination of the earliest stages in the development of this region, and I should have preferred not to mention them at all except that they confirm GOLGI and SALA'S view that the layers present a "disposizione inversa."

Certain appearances presented by the hippocampus at its extreme anterior end are highly suggestive of the folding over of the margin of the cortex into a pouch or trough; as is also the arrangement of the small cells in this region in animals in which the fascia dentata is rudimentary or not developed at all (see figs. 2 and 7). It does not necessarily follow, however, that the margin of the general cortex (subiculum hippocampi) rolls over into the trough in the manner imagined by GOLGI. It is clear that there is one other way in which the fascia dentata might be applied to the subiculum; the nucleus fasciæ dentatæ, or rod of large pyramids, might press against the outer side of the lateral wall of the trough. The fascia dentata would, in this case, be two-layered, and either its inner or its outer wall might be developed into nervous matter. Some appearances which I have seen, have led me to suspect that the fascia dentata is covered by a layer of undeveloped cerebral tissue (ependyma), but, on the other hand, in many cases an observation of the adult tissue favours the idea that the thickened margin of the general cortex has rolled over into the trough of fascia dentata. It is a question which can only be settled by ontological investigations.

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* HERRICK, "Cerebrum of Opossum." 'Jl. of Comp. Neurology.' February, 1892, p. 12.

† GOLGI, 'Sulla fina anatomia degli organi centrali del sistema nervosa,' pp. 80–112.

SALA* represents the fascia dentata as containing rounded cells, 10 to 20 μ broad by 15 to 30 μ long, which give an abundantly branched process towards the periphery, after the manner of PURKINJE's cells in the cerebellum. The nerve-network formed by the nervous process of the cells (which belong to GOLGI's Types 1 and 2) is in apposition with the nerve-network formed by the processes of the large pyramids of the nucleus fasciæ dentatæ. The small and large pyramids are therefore placed, as it were, back to back. As in many other cases in which portions of the brain are described and figured after the manner initiated by GOLGI, it is quite impossible to know how to harmonize or compare the descriptions with other observations. The beautiful pictures which accompany SALA's description show a single sheet of black cells, placed at considerable intervals apart, and each provided with an elaborately branched black peripheral process, and a single red central process which breaks up into an open network. The protoplasmic process unites with the processes of neurogleial cells. These pictures are, of course, drawn from mercury and silver impregnations. Prepared in any other way, the fascia dentata appears as a layer of "granules" close set in three or four rows, and mixed with a certain number of small fusiform or pyramidal cells (see fig. 1).

I agree, therefore, with GOLGI and SALA in looking upon the fascia dentata as a peculiarly-folded portion of the wall of the fore-brain, independent of the nucleus fasciæ dentatæ in its origin, and I am not disinclined to believe from such imperfect observations as I have been able to make into its mode of origin, that the layers may be inverted. We are not at present in a position to state, however, that an embryological inversion would permanently result in the projection of the processes of the neuroblasts in opposite directions.

I am absolutely opposed, however, to the writers just named, and, indeed, to all anatomists with whose works I am acquainted, in their attempt to homologize the elements found in the fascia dentata with those found in other parts of the cortex; or in other words to prove that the fascia dentata is a convolution comparable with other convolutions of the general cortex. *Firstly,* because in structure it does not appear to me to resemble the general cortex, and, *secondly,* because it does not behave like a convolution. For example, it does not vary in its development with the convolutions of the general surface. In perfectly smooth brains, the fascia dentata is as large, or proportionally larger, than in convoluted brains. As I have pointed out in my paper on the brain of *Ornithorhynchus,** the brain may be absolutely destitute of convolution, and yet the rhinencephalon be cut off from the general surface with unusual distinctness and the fascia dentata exceedingly broad. In the *Ornithorhynchus,* the fascia dentata lies wholly in the dorsal half of the cerebral hemisphere. It joins the pyriform lobe or rhinencephalon at the back of the porta. It is also interesting to notice that, since in this animal there is no corpus callosum, nothing has happened to destroy the external arcuate convolutions.

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* SALA, 'Zeitschrift f. wiss. Zool.,' vol. 52, 1, pp. 18–46.

If it could be proved that the stria longitudinalis lateralis passes anteriorly into true cortex as the gyrus geniculi, and posteriorly into the fascia dentata, a strong argument in favour of the latter being a convolution would be advanced, but the manner in which the fascia dentata terminates beneath the middle of the corpus callosum in strongly osmatic brains, such as that of the Ox, have led me to doubt the validity of this description, and the views held by VICQ D'AZYR (?), A. RETZIUS, ZUCKERKANDL, HONEGGER, GIACOMINI, *et al.* I fail to see any indication of the return of the fascia dentata to the under side of the splenium, in order that it may round the splenium and sweep forward in the nervus Lancisii in the manner required by the theory.

To label the fascia dentata, gyrus uncinatus, as is sometimes done,† appears to me a gratuitous assumption which does not in the least facilitate the comprehension of the subject. Its development bears no relation to that of the gyrus uncinatus, as can be seen at a glance in the brain of *Monodon monoceros,* in which the uncus and gyrus uncinatus (*seu* hippocampi) are particularly well developed, while the fascia dentata is absent.

A mystery surrounds the fascia dentata, which is not removed by attempts to homologize its several layers with those found in other parts of the cortex, and it would not serve my purpose to give in this paper a synopsis of the tables of homologies which have been drawn up by SCHWALBE, OBERSTEINER, GOLGI, and others. For purposes of comparison, it may be well, however, to give an account of the view generally held, as expressed, for example, by SCHWALBE, before appending a summary of my own.

SCHWALBE speaks of the fascia dentata as the remains of the gyrus arcuatus Arnoldi: ". . . der rudimentäre hintere untere Theil des Randbogens, der zwischen

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* HILL, 'Phil. Trans.,' 1893, p. 367.

† *Cf.* HERRICK, "Brain of Opossum," *loc. cit.*, figs. 4, 10, &c.

Fimbria und Subiculum cornu Ammonis gewissermassen eingefalzt ist und einen eigenthümlich gekerbten grauen Rand besitzt, als Fascia dentata Tarini."

He treats it as a part of the cortex, and gives a table to show the homology of the constituents of convolutions in general, the subiculum, the cornu Ammonis, and the fascia dentata. In this table the several constituents of the typical cortex are found in the fascia dentata by homologizing the fimbria and alveus with the medullary substance, the pyramids of the nucleus fasciæ dentatæ with the large pyramids, and the stratum granulosum with the layer of small pyramids.

It is easy to follow SCHWALBE in his distinction between the fascia dentata and the "cornu Ammonis," but very difficult to see where he can draw a boundary-line between the latter and the subiculum.

The writer's view of the relation of the hippocampus to the general cortex is entirely different, as he briefly pointed out in his translation of OBERSTEINER'S "Nervöse Centralorgane."* The fascia dentata cannot, he thinks, be homologized with any layer which is to be found in the cortex elsewhere. Instead of the fascia dentata being part of the layer of small pyramids—(1) it consists, as already pointed out, of "granules," and a much smaller number of pyramidal or fusiform cells; (2) it does not shade off into the cortex, but has a pronounced border on either side of the folded strip. Its upper border encloses in some situations a portion of the fimbria instead of its being everywhere (as it would be were it a portion of the general cortex) placed beneath the fimbria; (3) the nucleus fasciæ dentatæ is not the homologue of the layer of large pyramids, but of the whole cortex. As the hippocampus is approached through the subiculum, the many ranks of pyramidal cells arrange themselves in single file, the sheet thus formed enters the hilum fasciæ dentatæ, and, when within the fascia dentata, the pyramidal cells, which are not of exactly the same form or size as those in either of the layers of the cortex, form-up into an irregular crowd.

In certain sections of embryonic brains the cells of the nucleus fasciæ dentatæ are seen to belong to the series of the small pyramids, with which the large pyramids level-up from behind, as it were, and not with the large pyramids—so far as it is justifiable to describe these as forming a separate layer.

In early embryonic brains the thin mesial wall of the lateral ventricle is seen to be doubly folded. The portion of the S-fold which is convex towards the ventricle is the subiculum hippocampi, the deep concave part the fascia dentata; but a description of the way in which these structures are formed from these folds, and of how it comes about that they interlock, must be reserved until the matter has been more fully investigated.

The nucleus fasciæ dentatæ must, as I think, be regarded as the edge of the mantle proper; the fascia dentata as a sheath, into which this edge is received. In this sense the fascia dentata is a band of grey matter added to the cortex around a portion of its margin. It is useful to make a distinction between the cortex and the fascia dentata for descriptive purposes, albeit it is quite understood that both alike are developments from the wall of the fore-brain. I purposely use the expression "fore-brain," without the qualification "primary" or "secondary," since there are questions with regard to the development of this region which need, as it seems to me, further investigation.

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* 'The Anatomy of the Central Nervous Organs,' by OBERSTEINER and HILL, p. 362, *et. seq.*

The Hippocampus of the Ox.

I do not propose in this paper to give an elaborate account of the minute anatomy of the well-developed hippocampus, nor could I do so with advantage without a large number of illustrations. Before, however, describing the hippocampus, or rather the want of hippocampus, in marine Mammalia, it is necessary to call attention to certain points in the structure of a well-developed hippocampus, and it is desirable that the animal selected should be as nearly related to the Cetacea as may be, and that its brain should be of large size. It seemed to me, therefore, that I could not do better than select for my standard of comparison, the brain of the Ox.

In the Ox the outer margin of the slit through which the velum interpositum enters the lateral ventricle is folded over into the structure known as the hippocampus, of which the fimbria and fascia dentata are best regarded as parts. Commencing on the inner side of the temporo-sphenoidal lobe it passes backwards and upwards to the under side of the corpus callosum, which it joins some little distance in front of the splenium. It lies in contact with the corpus callosum to about its centre, when the folding over ends rather abruptly, by a rapid diminution in the extent of the folding, that is to say, the fimbriæ are then for a short distance separated from the corpus callosum by a small amount of grey matter only, after which, as the anterior pillars of the fornix, they sweep downwards along the back of the septum pellucidum.

Except for a distance of about 3 millims. the fimbriæ are separated from the corpus callosum by a considerable interval.

There are no posterior pillars of the fornix in the sense of pillars which intervene between the body of the fornix in contact with the corpus callosum, and the fimbriæ hippocampi.

The hippocampus presents no digitations at its inferior end similar to those which mark the floor of the descending horn of the lateral ventricle in the Human brain, and from which the comparison with the foot of the Seahorse was derived.

The hippocampus can only be described as a folding over of the cortex about the dentary fissure; its extreme edge ending in the fascia dentata Tarini, and its upper or convex surface bearing the fimbria, which gradually increases in thickness from its commencement at the apex of the ventricular slit.

A typical section through the *middle of the hippocampus* in the Ox has the following characters :—

As the cortex approaches the dentary fissure the arrangement of its cells is changed. If the section is really carried through the middle of the hippocampus, *i.e.*, near the splenium corporis callosi, where the caudex of the rhinencephalon is narrow, the change in arrangement commences at the ectorhinal (collateral) fissure. If it happened that the section was carried through the pyriform lobe a special description of the arrangement of the pyramidal cells would be necessary. On the outer or under side of the ectorhinal fissure, the molecular layer has a uniform thickness of ·4 millim., the pyramids are arranged, as everywhere else in the cortex, according to size, the largest being the farthest from the surface, but in a section taken from behind the pyriform lobe, it is sufficient to state that the cortex has its ordinary appearance.

In the gyrus hippocampi (*seu* uncinatus in the wider use of the term) the cells instead of forming a number of layers are pressed together into a sheet some two or three cells thick. The cortex falls rapidly outwards towards the lateral ventricle, from which it is separated by the thin sheet of white fibres known as the alveus. At the summit of the great curve upon which the fimbria rests, the cells are truly pressed into a single layer. Sweeping down for a short distance beyond the fimbria, the sheet of cells enters the hilum of the fascia dentata. As soon as this is entered the single layer gives place to a crowd of cells disposed with great irregularity, but still in most sections showing a tendency to concentration on its upper side (the concavity of the curve). Certain peculiarities in the form of the cells will be mentioned presently.

Where the cortex begins to fall back towards the ventricle its molecular layer is greatly increased in thickness, from ·4 millim. to 1·4 millim. It is not, however, increased in amount relatively to the superficial expansion of the layer of large cells, since it occupies the inside of a sharp curve. The molecular layer can hardly be said to enter the hilum fasciæ dentatæ.

The number of white fibres on the surface of the molecular layer also undergoes a considerable increase, the fibres lying tangentially for the most part and marking the boundary between the molecular layer of the cortex and the molecular layer of the fascia dentata, where these would otherwise be in contact beneath the bottom of the dentary fissure. Blood-vessels which enter from the bottom of this fissure also limit the two regions in certain sections. The names which have been applied to these several layers do not, as it appears to me, aid the description, but rather introduce a source of confusion by suggesting differences in kind, where there is only a change in the arrangement of the elements which make up the cortex in the subiculum hippocampi and other parts.

The only essential alteration consists in the disposition of the pyramidal cells in a thin sheet Between the bases of these cells and the ventricle lie the usual fusiform cells (stratum oriens) very few in number, the medullary substance (alveus), and ependyma. On the concave or mesial side of the curve lie the apical processes of the pyramids (stratum radiatum); the usual molecular layer, very thick, as already mentioned (stratum moleculare—I can see no object whatever in distinguishing the deeper part of it as stratum lacunosum); a sheet of white fibres such as are found elsewhere in the molecular layer, although not, perhaps, in such numbers; and then, as far as the bottom of the dentary fissure, the pia mater or surface-ependyma, from the cells of which remarkably coarse processes radiate into the substance of the cortex.

The fascia dentata I can only regard and describe as something superadded to the reflected cortex. It may, of course, be objected that, if the fascia dentata is a portion of the wall of the fore-brain, it is, *ipso facto,* a portion of the cortex, but this is a very unworkable definition of the term "cortex." It is far better to limit the name "cortex" to all such parts of the grey matter on the surface of the cerebral hemispheres as have a certain typical structure.

Portions of the wall of the fore-brain remain as "ependyma," other parts acquire the typical cortex structure, while still another part becomes the fascia dentata. The fascia dentata is a strip of tissue into which the thickened edge .of the cortex is received. It is almost uniform in thickness and constitution. Its borders are well defined, and show no tendency to shade off into the superficial layers of the cortex. If it could be stripped off from the border of the reflected cortex, it would be found to be a riband of uniform width and thickness; in the Ox about 9 millims. wide by 50 millims. long. Proceeding from the nucleus fasciæ dentatæ outwards it consists of the following layers:—(1.) The stratum granulosum which appears in most preparations as a sheet of nuclei some three or four deep, lying in clear spaces. The greater number of these nuclei belong to "granules." The sheet of nuclei comes quite to the surface on the mesial side. On the outer side it ends abruptly, and is in certain situations most clearly marked off from the adjacent molecular layer of the cortex by the fibres which occur in the superficial layer of the latter. (2.) The molecular layer has a thickness of ·4 millim. in its centre, but increases in thickness from its mesial to its outer border, and presents, so far as one can see, much the same constitution as in other parts of the cortex, unless it is, as I am inclined to think, somewhat more dense in texture. It is covered by (3.) the pia mater. Beneath the pia mater a few medullated fibres are to be seen running tangentially (stratum marginale).

Fig. 1 was taken from a portion of the fascia dentata of the calf from near the anterior end. The brain was hardened in warm bichromate of ammonia (2½ per cent.), well washed out in 30 per cent., 50 per cent., 75 per cent. alcohol, stained in carmine-alum *en bloc* (the excess of carmine being washed out in 30 per cent. alcohol), the tissue embedded in celloidin and cut frozen in gum. Sections were then stained with Weigert's hæmatoxylin method. The previous staining in carmine-alum causes the cells and their processes to take a black or grey coloration. It is a modification of Weigert's method which I introduced six years ago, and have since used almost invariably in my own work.

It may not be out of place perhaps to call the attention of histologists to the importance of stating how the tissue has been hardened before giving measurements of cells. Great confusion arises in the case of the central nervous system from want of information on this point, since we are often dependent upon accurate measurements of size for the only differentia between cells. Measurements are only comparable when taken from specimens of brains not only hardened in precisely similar ways, but of exactly equal freshness at the commencement of the process. In sections stained according to the manner just described the blood corpuscles are dark and regular in outline, and may serve, therefore, as a test of the amount of shrinkage which the tissue has undergone.

The blood-capillaries are numerous in the fascia dentata. They traverse it vertically or obliquely. The corpuscles in this specimen have an average diameter of 4 μ, *i.e.*, about half their size when living.

In examining the fascia dentata we have to look to the nuclei for information concerning the nature of the cells of which it is made up. The section stained as above described shows, in addition to blood corpuscles, four forms of nucleus.

1. Nuclei exactly similar to those found throughout all parts of the brain, 3·6 μ in diameter, round, darkly-staining. These are the nuclei of neurogleia cells. They are often seen to occupy the centre of a clear space, which indicates that the ground substance has shrunk away from them. It is important to bear this in mind when examining the granules, as otherwise one might be tempted to believe that the granules, which also occupy clear spaces, are surrounded during life by cell-bodies of exceedingly soft and deliquescent protoplasm which disappears in the hardening process.
2. Dark round or oval nuclei, 7 or 8 μ in diameter.
3. Clear dark-bordered nuclei 7, 8, or, in some cases (when oval) 12 or 13 μ diameter, with conspicuous nucleoli.

The differences between these two kinds of nuclei have exercised me for a long time past, not only when examining the fascia dentata, but in the cerebellum and elsewhere, but I am inclined to think that the marked contrast in appearance depends upon a different behaviour towards the staining-reagent, which again depends upon the age or state of activity of the nucleus. It will be noticed that a large number of the clear nuclei in this specimen, which was taken, as already stated, from a young animal, are in the act of dividing. I am inclined to think that we may safely conclude that the dark and clear nuclei both belong to granules, but that the former are in a resting condition, while the latter are either about to undergo or have recently undergone division.

4. Oval or triangular nuclei of 10 or 11 μ in long diameter. They are surrounded by cell-bodies, 18 to 20 μ in long diameter, and resemble very closely the small pyramids of the cortex. Measurements of a considerable number of these cells, as well as of small pyramids seen in the cortex in this section, give their nuclei an advantage in length of 1·5 μ, as compared with the small cortical pyramids; their cell-bodies are also slightly wider and shorter, but I do not think that any conclusions can be drawn from such trifling differences.

Occasionally a much larger pyramid, wide and blunt in form, is to be found in the fascia dentata. Only one such is exposed in the section under description. It measures 22·2 μ by 18·5 μ. It appears to be a displaced cell of the nucleus fasciæ dentatæ.

The ground substance of the fascia dentata constitutes an open network. The method of staining adopted, resolves it, as it does other parts of the cortex, into a soft brown substance, containing blue dots and dashes. I am not prepared, in this paper, to enter into the meaning of this appearance, but will merely point out that within the fascia dentata the brown substance contains more of the indescribably delicate blue tissue than it does elsewhere, and the latter has, in a certain degree, the appearance of lines disposed vertically to the layer.

The Nucleus Fasciæ Dentatæ.

As the sheet of pyramidal cells turns over beneath the fimbria, a notable alteration in the shape of the cells is apparent. In the middle of the subiculum the cells are rather smaller than elsewhere. In its upper part they are long pyramids 14 μ in transverse diameter. As the fimbria is passed they become equilateral or irregular and stellate, with a diameter of 18 or 19 μ.

It becomes in consequence difficult to say in which direction their apical processes, if they have any, point. The longer axis of the most superficial cells is, except at the apex of the nucleus, usually placed tangentially to the fascia dentata.

The nuclei of neurogleial cells are scattered over the section in about the same number as in other parts of the cortex. Of other nerve cells there appear to be none.

The ground substance is very transparent and uniform, and embeds a remarkably rich plexus of nerve fibres, which cross one another in all directions. Between the nucleus fasciæ dentatæ and the fascia dentata a large number of delicate fibres are disposed parallel with the surface.

Termination of the Hippocampus at its Anterior End.

As it approaches the temporal pole the hippocampal formation, considered as a whole, curves inwards towards the median line. It is not sufficient therefore to cut sections in a coronal plane, but the sections must, if they are to be comparable, be gradually inclined forwards on the outer side until they cut the coronal plane at an angle of about 45°. Misleading results have been obtained by continuing to cut the Human hippocampus coronally right up to its anterior end. A section of the "claw" ("digitationen") is obtained in this way. Although it expands in front its true anterior end lies on the surface of the brain and not within the ventricle.

My sections through the anterior end of the hippocampus of the Ox follow one another at varying intervals until the region in which the hippocampus terminates is nearly reached, and then I retain all the sections until the region is passed.

In the way in which the hippocampus progressively decreases in size I can recognize no point which calls for particular comment. Until it is very small it presents all the usual features which mark the folding over of the cortex and its ensheathing in fascia dentata. The mesial and lateral limbs of the fascia dentata are about equal in length. The mesial portion of the granular layer cuts the surface. The layer of pyramidal cells is disposed in the usual manner and shows no indication of a fusion with the fascia dentata.

The hippocampal formation is continued beyond the extremity of the descending horn. It is marked off from the general surface of the temporal lobe by a groove; the continuation forwards of the dentary fissure or the fissure about which the uncinate convolution (of microsmatic animals) curves over into its uncus. This groove is to be seen on the mesial surface of the pyriform lobe for a short distance in front of the termination of the hippocampus. In it lie some small blood-vessels.

At its extreme anterior end the fascia dentata is continued up the mesial surface of the pyriform lobe for about twice as far as it is a millimetre farther back. It loses its outer limb and is, as it were, DISPOSED FLAT ON THE SURFACE INSTEAD OF BEING DOUBLED UPON ITSELF around the pyramidal cell-layer. The layer of pyramidal cells is no longer folded upon itself, and it and the fascia dentata fuse at their dorsal borders, and are continued up the surface as a very indefinite sheet of small cells, larger than those of the fascia dentata but small for pyramids. The cells are also rather fusiform than pyramidal, with their long axes disposed tangentially upwards and downwards.

It is to be remembered that we are now in the region of the nucleus amygdaleus which occupies the anterior end of the rhinencephalon, filling up its temporal extremity (the natiform protuberance) and running forward beneath the frontal region as the pyriform lobe, or crus, of the olfactory bulb.

Termination of the Hippocampus behind or above.

In the Ox the folding-over of the margin which forms the hippocampus extends about half the length of the corpus callosum on its under surface, and then comes to an end somewhat abruptly 3 millims. to 4 millims. before the anterior pillars of the fornix leave the under surface of the corpus callosum. The splenium corporis callosi extends for some distance behind the hippocampus, the interval between the two being occupied by a bulging or tubercle of the gyrus fornicatus (callosal convolution).

A section through the posterior part of the corpus callosum shows the fimbria borne at some distance from the corpus callosum on the surface of the reflected cortex. The alveus is very extensive. Its white fibres sweep outwards and upwards to join the corpus callosum, as well as downwards into the fimbria; about the same number of fibres going apparently in each direction.

The fascia dentata is shaped like an arrow-head, as seen in section, its hilum is comparatively narrow, its nucleus well-developed, the large nerve-cells being uniformly distributed. A thin sheet of fibres separates it from the surface of the subiculum.

The strata granulosum et moleculare end abruptly at the margin of the fimbria, which is, of course, of great size (8 millims. high by 4 millims. wide at its base, as seen in section) in this region. A number of scattered bundles of longitudinal fibres are found inside the sheath of fascia dentata, beneath its upper or mesial limb.

The cells of the nucleus fasciæ dentatæ are considerably larger than any of the pyramids to be found in the cortex of the subiculum. They have an average diameter in the hardened tissue of about 40 μ, and are almost as broad as they are long: whereas the largest cells of the cortex of the subiculum at this level are not more than 12–14 μ in transverse diameter.

The stratum granulosum in this region contains about one pyramidal cell (diameter 8 or 9 μ) to ten granules, only the diameter of the nuclei of the latter can be determined, since their cell bodies are never so distinctly visible as to be clearly defined from their neighbours.

The folding over of the cortex ceases abruptly at the spot indicated, the outer edges of the two folds making an angle of 60° with one another. At neither end, therefore, does the hippocampus show a gradual transition from the general cortex of the brain. Allowing for the shortest distance necessary, so to speak, in ending the fold, the hippocampal formation is well and comparatively evenly developed in its whole extent.

HYPEROODON ROSTRATUS. (Figs. 2, 7, 8.)

I have for some time been acquainted with the peculiarities of the hippocampus in the brains of aquatic Mammals as illustrated by the Porpoise; on which subject I read a paper at the meeting of the British Association, in Manchester, in 1887. The Porpoise, however, has a rudimentary hippocampus, and my investigations would have been incomplete and conclusions uncertain, had not Mr. ROBERT GRAY, of Edinburgh University and Aberdeen, brought me from the Arctic regions five brains of *Hyperoodon* and two brains of *Monodon* in a capital condition, not only for macroscopical, but also for microscopical study. To take out the brain of the Whale and to detach from it the hippocampus are tasks requiring a very considerable knowledge of its anatomy, and I am deeply in Mr. GRAY's debt for bringing me specimens, removed without injury and so admirably preserved, as to allow of the use of WEIGERT's staining-method.

Certain peculiarities in the general form of the Cetacean brain as well as in the topography of its hippocampal regions need to be explained before an effective comparison can be made between this absolutely anosmatic and an ordinary osmatic brain.

The Cetacean brain is, as has so often been remarked, extremely convoluted, its fissures being of great depth. This renders the orientation of the brain difficult at first, but a very little study enables one to distinguish the primary and secondary from the tertiary fissures.

A still more remarkable peculiarity of the Cetacean brain is its wide departure in general form from the ordinary type.

The shape of the brain of my three uncut specimens is in each case distorted by the pressure of the muslin in which, as in pudding bags, they were suspended in a tub of spirits. The result was at first sight most perplexing, the whole brain being a blunt cone, its base completely hidden out of view by the orbital region, so that the medulla oblongata seemed to enter the base of the cone between the cerebellum and the frontal region of the cerebral hemispheres. The measurements of the cerebrum were in one specimen: Height, 7½ inches; length, 5¾ inches; transverse diameter, 8¾ inches.

Unlike any osmatic brain, the length of the Cetacean brain would appear from this specimen to be less than either its height or its width.

When I compared my specimens with the plates in KÜKENTHAL's 'Walthiere'* I felt convinced that exquisitely as KÜKENTHAL has figured the brain in this sumptuous monograph, he has doubted the possibility of so wide a departure from the ordinary

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* 'Vergleichend-anatomische und entwickelungschichtliche Untersuchungen an Walthieren,' von Dr. WILLY KÜKENTHAL. Jena, 1889.

Mammalian type, and has conventionalized the brain by somewhat flattening it down and opening it out. With a view to determining its natural form I prepared casts from the interior of two skulls in the Cambridge Museum, of one of which fig. 8 is a photo-lithograph.

The extreme measurements of this cast are: Length, 183 millims.; height, 160 millims.; transverse diameter, 266 millims.

It shows that the brain has the form of a truncated cone, the apex of the cone being directed upwards and but slightly backwards. Its peculiarity in shape has been considerably exaggerated in my spirit-hardened brains.

Inside the skull-case the cerebro-spinal axis presents the ordinary S curvature, but in an unusually marked degree. From the foramen magnum to the pons Varolii the medulla oblongata is directed ventralwards. The plane of the base of the brain, as a whole, makes an angle of 160° with the chief axis of the skull. The long axis of the cerebral cone is vertical to its base.

This is the form of the anosmatic brain exhibited in the highest degree, and is clearly due to two causes (1) the absence of the portion of the brain connected with the olfactory sense, and (2) the closing up of surrounding parts which have not this olfactory portion to displace and support them.

In the long brain of an osmatic animal, as is well seen in the Ox, although it is, of course, still more obvious in the brain of a Carnivore, the convoluted portion of the hemisphere is spread out, as it were, upon the unconvoluted, or almost unconvoluted, rhinencephalon. In the Human brain the rhinencephalon is reduced in size to the comparatively insignificant hippocampo-uncinate convolution. The Seal closely resembles Man, as will be pointed out subsequently, in the reduction of its olfactory brain. Every gradation between the Dog and the Whale, as regards the relative development of the olfactory brain, is to be found in the Mammalian class, and allowing for the total size of the brain, its size relative to the cross-section of the medulla, and other circumstances which have yet to be discovered, it is probable that the relation of breadth to height to length, or, as it might be expressed, the mean of the length-breadth and length-height indices of the brain would give a fairly accurate numerical expression for the development of olfaction in different species of animals.

It must not be supposed, however, that the only parts of the brain unrepresented in anosmatic animals are the rhinencephala. As I have attempted to show elsewhere,* the brain, in its general sense, is a formation of grey matter secondary to the grey matter of the axis or grey matter bordering the central canal. The "peripheral grey tube," as I termed it to distinguish it from the "central grey tube" which contains the primary centres of peripheral nerves, is disposed about the axis, and the loss of a cerebral nerve means the curtailment of both tubes as well as of all intra-cerebral connections between the missing parts of the two tubes. The short brain of the Whale is not only devoid of rhinencephalon, but its central grey matter also is shortened; the intervening white matter is absent; the great brain is reduced from an apparatus connected with five senses to an apparatus in which four only are represented, the missing sense being the one which in macrosmatic animals (Carnivora especially) demands the largest share in cerebral organization.

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* 'Plan of the Central Nervous System.' Cambridge, 1885.

I am not prepared, in this paper, to consider what other parts of the brain are absent in the anosmatic Whale; it is a large subject, which demands extensive and accurate investigation. It is, perhaps, worth while to point out, however, that there is great risk of error in concluding that parts absent in certain brains are directly connected in those animals in which they occur with the missing sensory apparatus; take the anterior commissure as an example.

The anterior commissure is present in the Whale, although extremely thin. It does not, however, follow from this that the anterior commissure is a chiasm between the olfactory nerves or tracts. Its enormous size in Monotremes and Marsupials precludes the possibility of this as a complete explanation of its function. The anterior commissure is certainly the commissure between the temporo-sphenoidal lobes, whatever other sets of fibres it may contain. The sense of smell has its cerebral representation in these lobes.

In the Whale, the temporo-sphenoidal lobes are reduced to a minimal size, and their commissure is correspondingly deficient.

The extreme retraction of the temporo-sphenoidal lobe produces an alteration in the disposition of the parts of the brain, which must be thoroughly understood before an attempt is made to cut a series of sections through the hippocampus which will be comparable with the series cut through this region in the brain of the Ox. The posterior limb of the fissure of Sylvius, instead of sloping upwards and backwards, as in other Mammals, passes almost directly upwards towards the apex of the conical brain. This is due to the fact that the temporo-sphenoidal lobe reaches so short a distance forwards on the basal aspect of the brain that the frontal lobe is allowed to roll round, as it were, into the place on the basal aspect usually occupied by the temporo-sphenoidal lobe. The posterior pillar of the fornix, and its continuation the fimbria, are continued in a very open curve backwards and downwards without any tendency to return. If, therefore, a section of the hippocampal region is to be compared with a coronal section of the brain of a Sheep or Dog, it must be made in a plane extending backwards almost horizontally with regard to the plane of the corpus callosum.

The body of the fornix and its posterior pillar are adherent to the under surface of the corpus callosum. In the middle part of its course it can be detached, for its fibres are here collected into a compact bundle placed at right angles to those of the corpus callosum. At its posterior part the fibres evidently spread out in a fan on the under surface of the corpus callosum, and the posterior pillar is marked by a groove on either edge, but is otherwise quite indistinguishable from the fan of fibres upon which it rests. If it be compared in this respect with the brain of the Ox already described, the extreme importance of this feature will be at once recognized; for in the Ox no part of the fornix is really in contact with the corpus callosum. As the hippocampus is approached, the rounded inner margin of the forceps posterior crosses the posterior pillar of the fornix very obliquely, passing into the substance of the hemisphere on its outer side.

The length of the hippocampal region is inconsiderable. In a large brain, weighing (in spirit) 1904 grms., in which the longitudinal distance from the genu to the splenium was 36 millims., and the length of the posterior pillar of the fornix (or rather the structure which would be the posterior pillar in an osmatic brain), from the point at which it diverged from its fellow to the attached portion of the fimbria, was 52 millims., the length of the fimbria properly so called—that is to say, of the portion of the fornix which adhered to the hippocampal convolution—was only 11·5 millims. Indeed, this measurement is considerably in excess of the length of the real hippocampal region. The posterior pillar of the fornix never leaves the under surface of the corpus callosum, but adheres closely to its posterior wing or tapetum. Instead of forming, for a considerable part of its course, an independent rounded column, it consists merely of fibres, not very obviously collected into a bundle, which, having begun to diverge from the middle line at some distance in front of the posterior border of the corpus callosum, pursues a long oblique course before it gains the margin of the forceps posterior. The length of the folded portion of the edge of the cortex, the hippocampus properly so called, and therefore the region in which alone the posterior pillar should be named the fimbria, did not exceed 9 millims. Of the exact measurement I am doubtful, for two reasons: *firstly*, as will be explained later on, it is very difficult to determine the exact point at which the cortex ceases to fold over upon itself; and, *secondly*, the measurements depend upon the estimated thickness of the sections. It may, however, be taken as certain, that the length of the border of the cortex which is folded over in the manner which marks the cornu Ammonis, and carries the fimbria, is at the outside 10 millims. Closer measurement is not necessary for purposes of comparison, for, if we compare the dimensions of the region in the anosmatic Cetacean brain with its dimensions in a megosmatic brain, such as that of the Ox, we find the most striking difference. In an Ox brain weighing (in spirit) 315 grms., the length of the cornu Ammonis, properly so called, was 50 millims.

Hippocampus of Hyperoodon rostratus.

Series of sections of this region were made from two separate brains. The second was the more satisfactory and therefore the sections from this series need alone be described. It was not convenient and did not happen to be necessary to make a complete series. The region was however divided into nine blocks, and from each of these a number of sections were taken (*a*) from the front, (*b*) from the middle, (*c*) from the back of the block. It yielded therefore twenty-seven sets of sections by which it may be said to have been completely explored. Some sections from each set were stained in carmine, and others in carmine and subsequently by WEIGERT's method. Of the WEIGERT-sections some were bleached in ferridcyanide of potassium and others in permanganate of potassium.

The hippocampal convolution commences with a sharp point which is deeply buried in a fissure between the flat posterior pillars of the fornix and the convolution which lies on the mesial side of the collateral fissure. To use any terms other than gyrus hippocampi (or uncinatus) and collateral fissure appears to me pedantic. Although the sense of smell is moderately present in Man, its development is so small as compared with the prominence of the same sense in most other animals that his microsmatic brain approaches in form the anosmatic brain of the whale so closely as to leave no possible doubt as to the homologies of these parts. There is no doubt in my mind as to the homology of the ectorhinal fissure of the Dog with the collateral fissure of Man, and consequently of the pyriform lobe and natiform protuberance of the Dog with the uncinate gyrus (or hippocampal gyrus plus the uncus) of Man, but a very large series of brains is needed to help one to realize such an extreme variation in development of corresponding parts.

From its position at the bottom of a deep recess the gyrus hippocampi gradually emerges on to the surface and at the same time steadily increases in width; or in other words the fimbria (posterior pillar of the fornix) inclines outwards into the descending horn of the lateral ventricle. In sections from block 8 the fimbria appears as a broad flat strap constricted in the middle like a Naples biscuit. In section 6 the outer limb of the biscuit is much narrower, the hippocampal convolution reaches as far outwards as the under side of the bay between the two limbs. The ependymal wall of the ventricle is attached to the lateral border of the outer limb so that the whole of the fimbria is outside the ventricle. The two rounded ends of the biscuit give place to ridges triangular in section, the mesial ridge being the first to appear. In block 4 (fig. 2) the gyrus hippocampi lies entirely on the mesial surface, the inner ridge is raised on to the top of its convexity; the outer ridge carries the ependymal wall on its apex. In block 3 the mesial ridge has disappeared, the ependymal ridge is small; in block 2 the fimbria is completely lost, no ridge marks the attachment of the ependymal wall. At its first appearance in block 8 the gyrus hippocampi is simply the edge of the cortex.

As the gyrus grows, traces of the reflection of the edge of the cortex down its surface are seen, but so extremely indistinct is this reflected portion that it is made out with great difficulty. It consists only of small triangular cells sparsely scattered in a single layer upon the surface of the molecular layer. The sheet reaches almost down to the collateral fissure. A little farther forward a slight condensation of the molecular substance is visible, and it is seen that the boundaries of this area are marked both outside, inside, and below by scattered small pyramidal cells. By block 5 we have therefore the vestiges of a fascia dentata, but so extremely indistinct is this formation that it was only after long searching that I discovered the existence of any differentiation whatever within what seemed at first to be the molecular layer of the hippocampal gyrus. It is not till we reach the front of block 4 that we come across any definite trace of the layer which is in osmatic animals the fascia dentata. In this block the layer begins to ascend the hippocampal gyrus so as to leave a space between its inferior border and the collateral fissure. Its inferior border is in 4A received into a cup of ependyma.

So delicate are these transitions that one would like to reproduce a section from both blocks, but it is as well perhaps, since the number of figures must be limited, to reproduce a section from near the back of block 4, from the region that is to say which lies immediately behind the more definite vestige of a fascia dentata.

4B (fig. 2) is the most posterior of the sections taken from near the middle of this block 4.

While in this section the folding over of the surface is very indistinct, in the sections immediately in front of it the rudimentary hippocampus, or, rather, the part of the cortex which would be hippocampus if ensheathed by fascia dentata, is as strongly developed as anywhere in the Whale's brain.

It shows the mesial wall of the ventricle from the collateral fissure up to the ventricular slit.

The fimbria is divided into two ridges, separated by a groove. To the summit of the outer ridge is attached the ependyma-wall of the ventricle, which is involuted to support the choroid plexus.

The ventricle is lined by a very thick ependyma, and a similar layer of epithelium covers the surface of the brain, although it is only seen in perfection in the fissures, being, as it were, stretched almost out of existence on the convexity of the convolutions.

The cells are conical; their nuclei lie close beneath the surface. The cells constitute a palisade, but, although their bases are in apposition, they do not constitute a membrane in any proper sense of the word; indeed, I am inclined to think that gaps are left between the bases of the cells through which the cerebro-spinal or subarachnoid fluid is allowed a free communication with the intercellular spaces of the brain-substance. The apex of each ependymal cell is prolonged into a tapering process, usually crooked, and therefore soon lost from the section, but sometimes straight and traceable for a very long distance into the brain tissue.

The greater number of fibres on the ventricular side of the cortex run tangentially, but especially near the surface layers of longitudinal fibres are visible. The layer of fibres is very thick, occupying nearly one-half of the thickness of the ventricular wall.

The layer of pyramidal cells, which has made a wide sweep into the region from beneath the collateral fissure, shows just at the level of this fissure a tendency to break mesially towards the surface. This curve is very pronounced, as will be seen directly, in the more anterior sections, where it constitutes the bottom of a cursive Q, of which the upper curve is formed by the reflected cortex.

For a very short distance the pyramidal cells are condensed into a thin stratum, foreshadowing the single-celled sheet of the subiculum, but above this, again, they are massed together in many layers. The sheet of pyramidal cells is carried mesially beneath the fimbria until it almost cuts the surface, the last of its cells being only 18 millims. from it.

The molecular layer is very broad in the gyrus hippocampi, but shows, as far as I can see, no peculiarities in structure. Near its surface are seen the few small pyramidal cells which undoubtedly represent the fascia dentata; none of them exceed 12 μ in diameter, while the pyramids in the subiculum have an average diameter of about 20 μ.

In section 3B, which is represented diagrammatically in fig. 7, the hippocampal formation is as well developed as anywhere. The layers of pyramids in the cortex are not concentrated to the same extent as in the subiculum of an osmatic brain, but still they are reduced more nearly into a single sheet in this situation than they are elsewhere. The cortex is folded outwards abruptly towards the ventricle. It then returns upon itself beneath the fimbria, and shows at its edge a little tendency to fall over towards the aborted fascia dentata.

In block 2 the cortex, as well as the aborted fascia dentata, are caught up on to the mesial surface of what would otherwise be the ependyma-wall of the ventricle. The hippocampus is, that is to say, continued forwards beyond the anterior end of the ventricular slit.

In block 1 the hippocampus has disappeared.

The most remarkable result of the examination of the hippocampal region of the brain of this animal is the discovery that at no spot in the region is there any fascia dentata. IN HYPEROODON, IN WHICH THE OLFACTORY BULB AND TRACT ARE COMPLETELY ABSENT, THE FASCIA DENTATA TARINI IS ABSENT ALSO.

It may appear at the first moment as if this result were simply a confirmation of ZUCKERKANDL'S generalizations, which are based upon observations made—not, of course, upon a series of sections such as I have just described—but upon a superficial examination of the brains of a number of Mammals, including the Dolphin.

This is the case in a very limited sense, however, as will be made clear by an analysis of ZUCKERKANDL's results. Such an analysis will necessarily include reference to certain large questions which I wish in this paper to avoid as far as possible. The subject to which I wish to restrict myself is the anatomical constitution of the hippocampus, and more particularly an exact determination by means of series of sections of the extent to which the fascia dentata is developed in the marine Mammalia.

ZUCKERKANDL commences his summary of the olfactory lobe as follows:—[*]

"Die Rindentheile des Gehirnes, welche in dieser Monographie behandelt werden, haben in gesammt Beziehungen zum Centrum des Geruchsorganes. Was bisher als centrale Stätte dieses Sinnesorganes angesehen wurde, ist zum grössten Theile im Gyrus fornicatus enthalten, und indem ich vor Allem über diesen berichte, wird es möglich, zu übersehen, wie weit zur Zeit die Lehre von dem Centralorgane des Geruchsapparates gediehen ist. In der Beschreibung desselben halte ich mich hauptsächlich an BROCA's ausgezeichnete Schilderungen, welche den Gegenstand erschöpfend behandeln."

BROCA's position is extremely clear, but, as I have tried to show elsewhere,[†] absolutely untenable.

BROCA[‡] associates the gyrus fornicatus with the rhinencephalic lobe (pyriform lobe, &c.) in a "grand lobe limbique qui peut donc être comparé à une raquette dont l'annèau entourant le seuil de l'hémisphère, est formé en haut par le lobe du corps calleux, en bas par le lobe de l'hippocampe et dont la queue est formée par le lobe olfactif." The handle of the racquet is supposed to be formed by the olfactory lobe and its peduncle, while the two striæ diverge to embrace the bat; the mesial stria going to the gyrus fornicatus, the lateral stria to the hippocampal lobe. The great limbic lobe is described and figured as the olfactory region. The proof of this conception is supposed to be based upon comparative anatomy, but the only witnesses whose evidence would be of value (the animals, namely, in which the sense of smell is not developed) are rejected on the ground that "la psychologie des Cétacés est actuellement (et pour longtemps sans doute) trop inconnue pour que l'on puisse savoir ou présumer quelles sont ces fonctions cérébrales qui se sont développées chez eux au delà du degré que l'anatomie permet d'admettre chez les autres animaux."

BROCA's great limbic lobe is an anatomical assumption, which is certainly not justified by the relative development of its parts in animals in which the sense of smell is prominent in different degrees. Nor is it supported by the only investigation into the functions of the gyrus fornicatus which has been made as yet. HORSLEY and SCHÄFER* assign to this region the several areas for tactile sense; an allocation of function which will, if confirmed, prove that the middle portion of the gyrus fornicatus instead of being a portion of a limbic lobe is really the base of the great Rolandic lobe, which extends outwards across the surface of the brain and includes the paracentral lobule, parallel convolutions, and operculum, together with a portion of the regions adjoining. If this allocation of function is justifiable, the comparatively modest dimensions of the gyrus fornicatus in the limbless Whales is not to be wondered at. The gyrus fornicatus is, however, very far from diminutive in Cetacea.

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[*] *Loc. cit.*, p. 32.

[†] 'Plan of Central Nervous System,' Cambridge, 1885.

[‡] BROCA. "Sur les centres olfactifs," 'Revue d'Anthropologie,' 2e série, vol. 2, p. 386, and also "Le grand lobe limbique et la scissure limbique dans la série des mammifères," *idem*, vol. 1, p. 385.

ZUCKERKANDL endorses BROCA's view with a qualification,† "Die aufgezählten Resultate erlangen einen erhöhten Werth, weil sie den Rückschluss gestatten, dass wir die Rinde des Lobus hippocampi und des Stirnendes des Lobus Corporis Callosi als centrale Stätte des Geruchsnerven anzusprechen haben."

ZUCKERKANDL then goes on to describe, as already explained (p. 592), that within the ring of the limbic lobe there lies another convolution which constitutes the true "gyrus marginalis" or edge of the mantle. This marginal convolution is well developed in most animals and also in the Human embryo, but in adult Primates and Whales is partially rudimentary inasmuch as it is represented in its dorsal portion by the nerve of Lancisi only.

It consists of three segments, the fascia dentata Tarini (gyrus dentatus), gyrus supracallosus ("Lancisi'schen Streifen" when atrophied, as in Man), and gyrus geniculi (also included in the striæ Lancisii in Man).

Just in the same way in which BROCA's speculative union into a great limbic lobe of three lobes or portions of the great brain—lobus olfactorius, lobus hippocampi, lobus corporis callosi—falls to the ground when tested by comparative anatomy, so, also, is ZUCKERKANDL's association of fascia dentata, nerve of Lancisi, and gyrus geniculi, although attractive as a speculation, opposed to certain facts.

It is extremely desirable that the development of this region which surrounds the foramen of MONRO should be studied with such exactitude as would leave the question quite beyond the reach of doubt. Failing precise embryological and especially histogenetical evidence I feel some unwillingness to refer to the subject at all, but lest it should be supposed that I endorse ZUCKERKANDL's conclusion with regard to the wider question, I feel bound to point out certain considerations which militate against his association of the fascia dentata, nerve of Lancisi, and gyrus geniculi in a "marginal convolution." These considerations may be best set forth after a statement of GIACOMINI's views.

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* HORSLEY and SCHÄFER. "Record of Experiments on the Functions of the Cerebral Cortex," 'Phil. Trans.,' 1888, B., p. 1. BROWN and SCHÄFER, ditto, 1888, B., p. 303. FRANCE and SCHÄFER, 1889, B., p. 331.

† *Loc. cit.*, p. 40.

GIACOMINI's* description of this region agrees with ZUCKERKANDL's in general outline although differing in certain points. I have not, as already said, had the advantage of seeing the original paper, but TESTUT states that he is giving an account of GIACOMINI's views in his 'Traite d'anatomie humaine' (pp. 497 and 498), and adds, "J'ai contrôlé sur un grand nombre de cerveaux les recherches du professeur italien ; elles sont exactes." I quote from this book. In the Human brain, according to GIACOMINI, the fascia dentata terminates at its anterior end, after extending to the most anterior part of the fissure between the uncinate gyrus and its uncus, as follows:—"Arrivé là, il s'infléchit en dedans, sort du sillon et devient de nouveau visible à l'extérieur ; il contourne alors de bas en haut le face interne du crochet de l'hippocampe et disparaît, en s'atténuant de plus en plus, sur la face ventriculaire de ce crochet. Cette extrémité antérieure du corps godronné nous apparaît nettement, dans la plupart des cas, sous la forme d'une petite bandelette d'aspect gélatineux, d'une couleur cendrée, large d'un millimètre à un millimètre et demi. Nous l'appellerons, du nom de l'anatomiste qui l'a à la fois découverte et bien décrite, la bandelette de GIACOMINI." At its posterior extremity the fascia dentata is said to join the nerve of Lancisi in the following way:—"Il change d'aspect, de bosselé qu'il était, il devient lisse et uni ; il change aussi de nom et devient le fasciola cinerea. Sous ce nouvel aspect et sous ce nouvel nom, il se porte obliquement en haut et en dedans vers le bourrelet du corps calleux, le contourne de bas en haut, arrive sur sa face supérieure et se continue là avec les tractus longitudinaux de Lancisi, soit avec les tractus médians, soit avec les tractus latéraux."

ZUCKERKANDL and GIACOMINI agree, therefore, in regarding fascia dentata, nerve of Lancisi, and geniculate gyrus as three portions of the same convolution, the most internal of the annular convolutions, the margin of the porta. They differ as to the connection between the fascia dentata and nerve of Lancisi. According to ZUCKERKANDL, the callosal convolution constitutes the intervening segment ; according to GIACOMINI, the intervening segment is the fasciola cinerea, while the callosal convolution is a portion of the general cortex.

I hesitate to give my own views upon this question, because I have not yet investigated the matter, as I hope to do soon, in the only way in which it can be definitely settled, by studying (1) a number of fresh brains, (2) series of sections through this region carefully hardened ; (3) its development ; nor have I paid especial attention to the Human brain. I have, however, made a large number of sections of this region in the brain of the Ox, and also of certain Cetacean brains, and am opposed to the view that the fascia dentata, or tissue which belongs to the ring or convolution, out of which the fascia dentata is developed, is continued on to the dorsal surface of the corpus callosum on the following grounds :—

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* GIACOMINI. "Fascia dentata del grande hippocampo nel cervello umano," 'Giornale della Reale Accademia di Torino,' 1883.

1. The little convolutions which rest against the splenium corporis callosi are indubitably continuous with the atrophied convolution which lies at the bottom of the callosal fissure, and is known as the stria longitudinalis obtecta, *seu* lateralis, or nerve of Lancisi, when this last expression is not limited to the stria medialis, or to the white fibres which run along the inner edge of the stria lateralis.

The stria lateralis emerges from the callosal fissure, in many cases in Man, in most cases in animals, in which the corpus callosum is relatively smaller. It appears again on the surface, either above the genu or only in front of the genu, as the geniculate convolution.

These parts, callosal convolution, stria obtecta, supra-callosal and geniculate convolutions are parts of the general mantle, and do not resemble the fascia dentata in minute structure.

2. In the Ox (and many other animals) the callosal convolutions, when not strongly developed, very closely resemble in form the corresponding convolutions in any human brain in which they are unusually well developed; but their size, both in Man and animals, varies considerably. In the Ox, however, instead of the fascia dentata ceasing beneath the splenium at the spot at which fasciola cinerea and subcallosal convolutions appear, it accompanies the fimbria to within a few millimetres of the level at which the septum pellucidum intervenes between the fornix and corpus callosum. In other words, the *fascia dentata continues its subcallosal course* instead of accompanying the fasciola cinerea to the dorsal surface of the corpus callosum, nor can I see, in sections which I have made through this region, the slightest indication upon the under surface of the corpus callosum of any structure which might be regarded as the fascia dentata returning to the splenium to surmount it and join the nerve of Lancisi.

These considerations seem to me to indicate that the corpus callosum in its backward extension breaks through a convolution which lies outside the ring from which fascia dentata, fimbria and fornix are developed.

It is, so to speak, an accident that the fascia dentata terminates at the level of the callosal convolutions in Man.

Turning now to the more special point: ZUCKERKANDL's observations upon the fascia dentata. In the second edition of his 'Twelve Lectures' (I quote from the English translation),* EDINGER says, "All the convolutions which lie near the margin of the hemisphere—the gyrus fornicatus, the gyrus hippocampi, the stria longitudinalis Lancisi, and the fascia dentata—are very strongly developed in animals having highly perfected organs of smell. In those which, like human beings, have small olfactory lobes, they are somewhat atrophied, and in the Dolphin, which has no olfactory lobe, they are totally undeveloped (ZUCKERKANDL)."

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* EDINGER. 'Twelve Lectures on the Structure of the Central Nervous System.' Translated by VITTUM and RIGGS. Philadelphia, 1890.

ZUCKERKANDL in his paper makes the following references to the brain of the Dolphin, in all of which, except the last, he omits to make any mention of the fascia dentata:

"Cetaceen.—Es wurde nur der Delphin untersucht.

"A. Der verkümmerte lobus hippocampi besitzt einen Haken im Sinne der Primaten; die den Mandelkern enthaltende Rindenpartie liegt über dem lobus hippocampi.

"B. Die Balkenwindung,

"C. Die Randwindung, und

"D. Die Fimbria fehlen" (p. 19).

"Cetaceen.—Untersucht wurde der Delphin. Der gyrus marginalis fehlt bis auf das kurze Stück des dorsalen Schenkels, der in hohem Grade atrophisch ist" (p. 42).

"Bei den Cetaceen, Primaten, vielleicht aber schon bei einzelnen Halbaffen, ist die ventrale Portion der Randwindung relativ schwach, die dorsale hingegen auffallend atrophisch. Die Differenz zwischen den beiden Portionen des Randbogens is demnach auf einen atrophischen Process zurückzuführen. Am meisten atrophisch ist die Randwindung bei den Cetaceen und bei den nicht anthropoiden Affen" (p. 56).

"Cetaceen.—Untersucht wurde der Delphin. Von einer Balkenwindung ist keine Spur vorhanden" (p. 67).

In his chapter, "Ueber die Bedeutung der bisher beschriebenen Rindentheile und über das Gehirn des Delphins," we find this sentence: "denn hier findet sich sogar ein Rudiment der fascia dentata mit einem dicken stratum granulosum vor, wie aus der schematischen Zeichnung ersichtlich wird, in welcher der ganze Spitzenantheil des Hakens der Fascia angehört."

From the time of TREVIRANUS both comparative anatomists and pathologists have frequently noted the fact that absence or deficiency of the olfactory bulb is associated with deficiency of the hippocampus, using the term in its wider sense. This relation is confirmed by ZUCKERKANDL, to whom also belongs the merit of correcting the extraordinary errors made by TIEDEMANN,* who mistook the optic thalamus for the hippocampus; and STANNIUS,† who describes and figures (the figures are reproduced by ZUCKERKANDL), a hippocampus in the Dolphin formed upon the ordinary osmatic plan.

ZUCKERKANDL, however, sets out with a case to prove; to wit, that the outer arcuate convolution is developed into (1) the fascia dentata, (2) the gyrus supracallosus (or Lancisi's nerve), (3) the gyrus geniculi; the inner into the fimbria and fornix. The Dolphin is used as a proof that these three parts are proportionately developed and vary as the olfactory bulb, and the case, as based upon the Cetacea, breaks down on every count.

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* TIEDEMANN. 'Zeitschrift f. Physiologie,' vol. 2, 1827.

† STANNIUS. "Ueber den Bau des Delphingehirnes." 'Abh. a. d. Gebiete der Naturw.,' Hamburg. Quoted by ZUCKERKANDL.

1st. He says that in the Dolphin the fimbria is absent; it is present in all the marine Mammals which I have examined; the only specimen of the Dolphin's brain which I possess is not sufficiently well preserved for this investigation.

2nd. He says that the callosal convolution (Balkenwindung) is absent. With a brain which is not folded forward beneath the corpus callosum, and in which (more completely than even in Man) the posterior pillar of the fornix is adherent to the corpus callosum, there is no place for this small convolution on the back of the splenium, or between the splenium and the fornix.

3rd. The gyrus arcuatus (Randwindung) is absent. On the contrary, the stria lateralis presents much the same appearance as in other Mammals. It is present in Hyperoodon, Monodon, and Phocaena, and in the former it escapes from the position in which it is hidden at the bottom of the immensely deep callosal fissure and appears on the mesial surface as a narrow supracallosal convolution which ends in front in a gyrus geniculi. In one specimen in my possession, which has been beautifully preserved in bichromate of ammonia, the supracallosal and geniculate convolutions have much the same appearance as in the Ox. These convolutions, as well as the callosal (or subsplenial) convolutions, are subject to great variations in development. In the Anatomical Museum, at Cambridge, there is a large model of the anterior portion of the human cerebrum which I made for the purpose of illustrating a paper at about the time at which ZUCKERKANDL's article on the "Riechcentrum" appeared. I was at the time ignorant of ZUCKERKANDL's researches, and made the model from a fresh human brain in which the geniculate convolution happened to be remarkably well developed and its connection with the stria lateralis very clear. When ZUCKERKANDL's article appeared I abandoned the paper, finding that the work had already been done; but the examination of a considerable number of human brains and the comparison of the brains of Man and animals had shown me that the circumcallosal convolution is exceedingly variable. Its variability is strongly suggestive of alterations in the mesial aspect of the brain, produced by the backward extension of the corpus callosum.

The rudimentary condition of the nerve of Lancisi in Man and in Cetacea appears to me to depend not upon their union with the fascia dentata and association through this with the olfactory apparatus, but upon the large size of the corpus callosum.

4th. ZUCKERKANDL pays but little attention to the only structure which is absent or rudimentary in Cetacea, namely, the fascia dentata.

PORPOISE. (Figs. 4, 5, 6, 9, 10, 11.)

Although less conical than that of the Whale, the brain of the Porpoise (*Phocæna communis*) resembles the Whale's brain in general appearance. It is short, and extremely broad as compared with osmatic brains, being almost globular in form.

As in the Whale, the front part of the cerebral hemisphere is flexed upon the back part, although the base of the brain is not covered nearly so far as in the Whale. The surface is deeply fissured.

With a view to showing clearly the peculiarities in shape, which appear to me to be characteristic of anosmatic brains, I prepared a cast of the inside of the skull of a young Porpoise (fig. 9). It exhibits the extreme diminution of antero-posterior length with corresponding increase in breadth and height. Since the brain fits close to the skull case, such a cast represents accurately the shape of the brain; as is evident from the appearance of the fissures and convolutions upon all parts of its surface.

Its extreme measurements are: length, 80 millims.; height, 78 millims.; transverse diameter (of the two hemispheres), 132 millims.

General Form of the Hippocampus of the Porpoise.

The fornix is, in the Porpoise, quite distinct from the corpus callosum.

Its anterior pillar is well defined. The body, which is small and oval in section, is fused neither with its fellow nor with the corpus callosum. The posterior pillar is free.

It is difficult to say how far the fimbria reaches forwards, for it seems to die away on the uncus instead of being tucked in beneath it in the usual manner (see figs. 5, A, B, C); but the total distance from the point at which the posterior pillar first touches the cortex to the tip of the hippocampal region, in a large adult brain, was only 18 millims. The fimbria is strap-shaped and, in the greater part of its extent, completely covers the reflected margin of the cortex, but I estimate (from my sections) that the length of the reflected portion is about 10 millims.

Hippocampal Region in the Porpoise studied in a series of sections.

In its general features this region corresponds closely in structure with that of the Whale. The reflected layer of cortex is throughout feebly developed, small in all its dimensions, and pressed flat against the cortex of the gyrus hippocampi.

Section 9A (fig. 10) shows the form of the hippocampus in its posterior part.

The fimbria is flat. It does not, as in osmatic brains, take the form of a distinct rod, but is a flat band which covers the reflected portion of the cortex, and belongs distinctly to the sheet of fibres which lines the ventricle.

The pyramidal cells, which show in the gyrus hippocampi a tendency towards an arrangement in several layers, are collected at the point where the cortex folds over into a single layer, the cells in which are fairly large. In the reflected cortex the cells become fewer and smaller as the edge is approached.

There is no thickening of the layer into a rod (nucleus fasciæ dentatæ). Nor is there any trace, at this level, of the reception of the edge of the cortex into a scabbard of fascia dentata.

Small though it be, the fascia dentata is nevertheless distinct in section 5A (fig. 11). It consists, at this level, of some three or four layers of cells closely packed together. As in other animals the nuclei are of two kinds, nuclei of small angular nerve cells, and "granules," conventionally so called, *i.e.*, nuclei which are somewhat smaller and darker than those of the angular cells, and lie in clear spaces with but faint traces of cell bodies in tissues as ordinarily prepared.

The layer of fascia dentata, with its nuclei and superficial molecular stratum, does not fuse in any way with the layer of pyramidal cells; but there is not, on the other hand, any appearance from which the relation of the fascia dentata to the cortex can be inferred—whether a special development of some part of the cortex or a new formation superadded.

My sections do not, unfortunately, allow me to state with accuracy the length of the fascia dentata; but I can assert that it is found in the Porpoise for a short distance only (at the outside 6 millims.), and that it nowhere reaches a greater development than in the section (5A) which I have drawn.

HIPPOCAMPUS OF MONODON MONOCEROS. (Figs. 3, 12.)

The brain of the Narwhal resembles that of the bottle-nosed Whale so closely in those particulars, upon which in my account of *Hyperoodon* I laid especial stress, that I do not propose to call attention to them again.

Its extreme flexion is well shown in the accompanying rough sketch of the brain (fig. 12), as seen from the under side after cutting through the axis in front of the cerebellum. Looking at the sketch on the right side first, we see, in order, the corpus callosum (its splenium), the anterior right tubercle of the corpora quadrigemina, the posterior tubercle, the brain-stem with the fillet and crusta on its side; and lastly, on the extreme left, the optic chiasm. Owing to its extreme flexion, all these structures can be seen at the same time after the brain-stem has been divided by a single cut.

The uncinate convolution is larger than in *Hyperoodon*. It appears on the surface from beneath the forceps posterior of the corpus callosum, bends round the axis, and curves slightly round the temporal pole into the throat of the Sylvian fissure. The uncus is completely separated from the rest of the convolution (or as it would be expressed in the more usual terminology, the uncinate convolution is separated from the hippocampal convolution) by a deep fissure. It is oval in form.

The fimbria is not seen from the under surface of the brain, nor is it visible when the temporo-sphenoidal lobe is broken off and looked at from its mesial aspect. It is hidden away within the hiatus ventriculi (choroidal fissure).

Among the treasures which Mr. GRAY brought me from the Arctic regions were two brains of *Monodon.* They were hardened in bichromate of ammonia, and it was therefore possible to stain sections made from them in hæmatoxylin after WEIGERT'S method. Unfortunately, as so often happens, the chromic salt had rendered them extremely friable in texture, brittle almost to disintegration, and great care was therefore needed to fix any part which it was necessary to detach with a syrupy solution of collodion before cutting it.

The larger brain must, as I judge from its size as well as from histological evidence, have come from a young animal. The smaller brain is labelled "fœtal Narwhal." From its size, the complexity of its convolutions and the presence within it of medullated fibres and well formed nerve-cells, it is clear that the fœtus must have been at full term.

The right hippocampal region was removed from the larger brain and cut into a series of sections. From the smaller brain both hippocampal regions were cut up.

I had hoped to find in the fœtal brain evidences of development along the ordinary lines followed in osmatic animals, but could recognize no points which seemed to me to need illustration, and therefore confine my description to the brain of the larger animal.

The hippocampus of this animal was cut into ten blocks. Each block into three sets of sections (A, B, and C).

Section 6B (fig. 3) is a typical section through the region in which the nearest approach is made to the formation of a hippocampus. In order that the whole section might be shown in a figure of practicable size it is magnified only 9 diameters. This necessitates a slight exaggeration in the distinctness of its details; cells and fibres are shown with the same distinctness as when viewed through an objective magnifying 50 diameters. It was necessary also to make slight restorations in the section owing to the extreme tendency of the tissue to split, already mentioned. It is perfectly accurate, however, as a combination-view of three or four sections.

In the upper part of the figure are seen from left to right:—(1.) A part of the optic tract; this is an excellent landmark in all the sections; its fibres are much larger than any others which are cut across in the several sections. (2.) A part of the cerebral peduncle (substantia innominata) with a distinct bundle of fibres lying just above the attached border of the mesial wall of the descending horn; the tænia semicircularis.

In sections a little further forward, block 5, the tænia semicircularis and fimbria form a common sheet of fibres; a good many fibres running up and down the wall in the plane of the section. It is also useful to mention as giving a clue to the exact position of the sections, that from 3B, forwards, the anterior perforated space is recognizable on the outer side of the tænia semicircularis owing to the presence in the tissue beneath it of extremely large oval cells containing a patch of bright yellow pigment on one side of the nucleus. These are the peculiarly characteristic cells of the basal optic ganglion of WAGNER.

The ependyma wall of the ventricle is thick, and affords an excellent opportunity for the study of the modifications which epiblastic cells undergo when reduced in function to connective tissue purposes. On its outer side the connective tissue wall forms a mass of fibrous tissue as thick as a penholder, supporting a considerable number of large and a very great quantity of small tortuous vessels. The appearance which it assumes in all sections through this region, no matter to what animal the brain belongs, are, of course, largely due to contraction in the hardening agents.

The plate of velum interpositum is prolonged into two pouches, of which the mesial or lower pouch fits into the angle beneath the fimbria, while the upper or outer pouch fits into the pocket formed at the angle between the gyrus hippocampi and cortex, which is dipping into the collateral fissure.

The prolongation of the velum interpositum, beneath the fimbria, is a marked feature of all the sections. The fimbria, instead of lying as is usually the case on the summit of the hippocampus, lies altogether in the groove between the crus and the hippocampus, and takes the form of a flattened plate which covers over a prolongation of the descending horn. I have several times in this paper called attention to appearances which are suggestive of a deep folding of the cortex inwards and downwards (as the reflected cortex), and its return upon itself as the fascia dentata, fimbria, and ependymal wall. In the sections of the hippocampus of the Narwhal, I thought several times that I had come upon this folding, always to find, however, that it was due to the splitting of the section in the line of a blood-vessel which entered the cortex from the velum interpositum and traversed it from without inwards parallel with and very near to the surface of the summit of the hippocampal gyrus.

The presence of these blood-vessels which enter the cortex from the ventricle and run towards the surface in this region is remarkable, since the plan of blood-supply of the rest of the gyrus hippocampi, as of other parts of the cortex, is for the vessels to enter from the pial surface. It seems to point strongly to the existence in the embryo of a ventricular pouch which has closed up in the course of development.

The fimbria increases in transverse sections very rapidly from before backwards; retaining throughout, however, its strap-like form. As already mentioned, it is separated from the alveus by a deep groove or pocket. Another small groove marks off the portion of the alveus which lies beneath the fimbria as a separate column, more distinct in the sections behind 6 than in the section figured.

The sections show in a very striking manner, owing presumably to the fact that they are taken from a young animal, the way in which the fibres of the alveus take origin in the cortex of the hippocampal convolution, pass between its columns of cells, and sweeping inwards beneath the floor of the ventricle, curve round the groove between the alveus and fimbria into the fimbria, in which eventually they assume a longitudinal direction. In sections of osmatic brains the formation of the fimbria from the alveus is obscured by the origin of large numbers of fibres in the hippocampus proper, if it is allowable to restrict this term to the reflected cortex.* The fibres of the alveus are crossed at right angles by fibres which pass outwards into the white matter which lies beneath the collateral fissure.

A few delicate fibres are seen near the surface beyond the border of the pyramidal cell-layer, close to the fimbria. They are also found in the cortex of the gyrus uncinatus, but none are to be seen at the extremity of the gyrus.

In structure the cortex of the gyrus uncinatus resembles the cortex in other regions. As the hippocampus is approached the pyramidal cells are massed rather more closely together and reduced to a layer three or four cells deep, but no attempt is made to take up an arrangement in Indian file. At its very edge the layer is slightly thickened and turned downwards near the surface. The cells of the reflected portion of the layer are smaller than those in the rest of the cortex. For a short distance downward the cells of the reflected layer are pyramidal, angular and darkly stained; they then give place to cells which do not stain. In these cells, which are placed pretty close together, indications of cell bodies are visible; but as they are not stained, the form of the cell cannot be made out. Their nuclei are large and clear with a distinct nucleolus. They increase in numbers towards the inferior and mesial angle of the convolution. They resemble in appearance the cells, or rather the nuclei of the cells, found in embryonic cortex.

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* As pointed out in the introduction to this paper, the nomenclature of the region is in complete confusion. The term "hippocampus" or "hippocampus major" is used either for the swelling in the descending horn, or for this *plus* the fimbria and fascia dentata, or the terms "pes hippocampi" are used for the swelling and "cornu Ammonis" for the fimbria and fascia dentata, or cornu Ammonis includes the whole region, or again it is limited to the swelling in the descending horn. Some definition of these terms is absolutely necessary, but it is hardly possible without rearrangement to a certain extent. I am very unwilling to make any suggestions which may still further add to the confusion by introducing a new use of the words, but seeing that a certain formation of brain is found in osmatic animals which is absent in anosmatic animals, it appears to me most convenient to term the osmatic structure the "hippocampus," this being, so far as I can make out, the use which would have been made of the term by those who first described the region, had they known of the difference between the two classes of animals in this respect. I imagine that ARANTIUS or HALLER would have said: "the Dog has a very large hippocampus while the Whale has none." If then we use the term for the structure which the Dog possesses and the Whale does not possess, we have, at any rate, a useful anatomical distinction between the two. I should then do away with the term "gyrus hippocampi" altogether, for almost all anatomists confuse it with the gyrus uncinatus, and I should term the whole of the most internal convolution from the isthmus gyri fornicati downwards and forwards, the "gyrus uncinatus," with its hook, the "uncus." The ascent from the gyrus uncinatus to the fascia dentata I should term "subiculum hippocampi." The swelling in the descending horn has been known for three hundred years as "the hippocampus;" but then this term is made to include so much more that it has no definite signification, and there seems no reason against our terming it "pes hippocampi" for the sake of distinction.

The term hippocampus would then mean the reflected cortex, where its cells form a single sheet, with its enlargement into the nucleus fasciæ dentatæ, *plus* the fascia dentata itself, and the fibres derived from this region which pass into the fimbria. It may be objected that I include under the term hippocampus structures which by most anatomists are known collectively as fascia dentata; but my answer is that it seems to me highly misleading to include under this latter name two entirely different tissues—(1) the piece of the layer of large pyramids which is reflected as the nucleus fasciæ dentatæ, and (2) the particularly distinct layer of "granules" and molecular substance which ensheaths this rod of pyramidal cells.

It would be understood that the fimbria is made up of at least two distinct sets of fibres—(1) the fibres of the alveus which are derived from the uncinate gyrus; (2) the fibres which take origin in "the hippocampus."

In the Narwhal the cortex is reflected in the hippocampal region; but *no fascia dentata is developed.* Its place is taken by embryonic tissue. In an osmatic animal of the same age the hippocampus is relatively far larger and more conspicuous than it is in the adult.

HIPPOCAMPUS OF PHOCA VITULINA. (Fig. 13).

The brain of the Seal belongs to a strongly microsmatic type resembling in this respect the brain of Man. When it is viewed from the ventral side its general resemblance in form to the human brain is indeed very striking. It is almost as broad as it is long, and the orbital region of the frontal lobe is large, a considerable portion of the frontal lobe having rolled over on to the basal surface.

If the parts in which we are especially interested are examined, it is found that the olfactory bulb and tract are distinct although small. The tract ends in an external "stria" which skirts the outer edge of the anterior perforated space (tuber olfactorium). I was unable to trace the passage, so distinctly seen in macrosmatic brains, of the external stria on to the surface of the pyriform lobe.

The rhinencephalic lobe is small and tapers rapidly at its hinder end. The rhinal fissure joins the fissure of Sylvius, and then skirts the outer margin of the pyriform lobe as a deep posterior rhinal or ectorhinal fissure, which does not, however, run on into the equally deep collateral fissure, but is separated from the latter by transverse or bridging convolutions. So striking, however, is the resemblance to the human type, that there appears to be no sufficient reason for the use of a separate nomenclature for this region. I have already insisted that the pyriform lobe, including its natiform protuberance, is the same part as the uncinate (*plus* the hippocampal) convolution of human anatomy. Difficult as it is to recognize the homology between these parts in the macrosmatic Dog or Ox and microsmatic Man, the aquatic Mammalia supply all the intermediate steps. The crus of the olfactory bulb, or the pyriform lobe, as it is often termed by writers who distinguish between the pyriform lobe and the natiform protuberance, is represented in Man by the superficial region which intervenes between the internal and external olfactory striæ.

Adopting, therefore, the terminology of human anatomy, we should describe the uncinate convolution of the Seal as broad in front but bearing no uncus. The dentary fissure has a remarkable disposition, for, instead of ending between the uncus and the rest of the uncinate convolution, it is carried outwards and forwards around the anterior end of the temporo-sphenoidal lobe as far as the temporal pole. In *Monodon* the isolation of the uncus is still more complete.

When I examined the hippocampal region with the naked eye, I came to the conclusion that the fascia dentata was well developed, that it appeared on the surface beneath the fimbria and was continued forwards beyond the spot at which the fimbria disappears in the ventricular slit. Microscopical examination, however, showed this to be a complete mistake. The fascia dentata does not appear on the surface at all, but lies at the bottom of a deep dentary fissure. I had mistaken, as any one who looks at the surface of the brain is likely to do, the narrow roll of cortex which intervenes between the fimbria and the fascia dentata for the fascia dentata itself. It would be difficult to find a name for this portion of the cortex, which is, so to speak, a convolution turned inside out and exposing its medullary layer on the surface. In the Seal, therefore, the cortex is folded over further than in any other animal I have examined; the upper loop of the S (see fig. 13) almost completing the circle. The fascia dentata is hidden away at the bottom of the upper bay.

In consequence apparently of its position between two convolutions, the fascia dentata is much flatter than usual, its two limbs being pressed together so that they meet at an acute angle.

In my Section 4B, the hippocampal formation is shown at its greatest development. Its anatomical disposition is curious, the cortex making a very wide sweep before ending in fascia dentata. It might almost be supposed that the gyrus hippocampi lay at the bottom of the dentary fissure, but the arrangement of the pyramidal cells shows that this is not the case, since, as soon as the cortex enters the fissure, its cells are pressed together into a thin sheet of large pyramids with very long tapering apical processes, arranged with great regularity. The small pyramids disappear from the cortex at the same point.

This is the part of the gyrus hippocampi which might with propriety be called the subiculum hippocampi,* if the nomenclature of this region ever becomes entitled to claim anything like definiteness. It would be very useful to have a term which might belong to the cortex which has not yet entered the fascia dentata, but has undergone this change in the disposition of its layers of cells.

---

* The term subiculum cornu Ammonis vel hippocampi is used as synonymous with gyrus hippocampi; which, again, is the name applied by many anatomists to a part of the convolution termed by others the gyrus uncinatus.

The fascia dentata is ill-developed; it is relatively less extensive than even in Man. Its under (mesial) limb commences very gradually on the upper border of the dentary fissure, nearer to the mesial surface of the hemisphere than does its upper or external limb. Its granular layer appears to be made up of "granules" and small pyramidal cells in about the same relative numbers as in megosmatic brains.

In the greater part of its extent the hippocampal region presents the same features as in 4B. Slightly behind this level, however (5B), the mesial limb of the fascia dentata reaches the surface of the brain. In the sections behind this it is seen to be sharply folded upon itself and continued up the surface towards the fimbria for a short distance. The course of its folding is, therefore, as follows:—In the front, where it is deeply sunk in the dentary fissure, it is folded into a V. Behind this, the angle of the V gives place to a curve. Behind this again, the mesial limb is folded upon itself in a fresh place.

SUGGESTED TERMINOLOGY.

So much confusion arises from discrepancies in the use of the terms applied to the hippocampal region that I am inclined to suggest, even at the risk of adding to the confusion, a revision of the terminology on the following lines:—

The hippocampus to mean the whole of the region in which the border of the mantle bears fascia dentata.

The most internal convolution, from the inferior end of the gyrus fornicatus (isthmus gyri fornicati) onwards, to be termed gyrus uncinatus; its hook the uncus.

The homologous region in megosmatic brains to be termed the pyriform lobe; this term to be synonymous with rhinencephalon, excluding the olfactory bulb. The pyriform lobe to be divided into its crus, the natiform protuberance, and its caudex or posterior tapering portion.

The term gyrus hippocampi to be discarded.

Subiculum to mean the portion of the cortex of the uncinate gyrus in which changes preparatory to the formation of the hippocampus are recognizable, *i.e.*, the concentration of large pyramids and the absence of small ones.

The swelling in the floor of the descending horn to be termed the pes hippocampi; the sheet of white fibres which covers its surface the alveus.

The reflected portion of the cortex, or portion which returns upon itself, declivus hippocampi; its thickened border, nucleus fasciæ dentatæ.

The expression fascia dentata to be rigidly limited to the layer of small cells (zona granulosa) and its superficial molecular layer.

The fimbria hippocampi to be reckoned as a part of "the hippocampus" in the general sense suggested above.

Dentary fissure to be the fissure between the subiculum hippocampi and fascia dentata.

The term hippocampal fissure, which at present is sometimes used as synonymous with dentary fissure (in the sense just defined) and sometimes for the slit by which the choroid plexus enters the descending horn, to be abandoned.

Hiatus ventriculi (rather than choroid fissure, or lateral portion of rima transversa cerebri) to be the name for the slit by which the descending horn would be placed in connection with the subarachnoid space, were it not closed by the ependymal wall of the ventricle.

I do not pretend that such a terminology is as satisfactory as it might be made, were it possible to overlook terms the use of which is already more or less fixed by custom, but with the exception of the introduction of the terms caudex and declivus (which are already well-known anatomical words) and the substitution of hiatus ventriculi for the confusing expression fissura choroidea or fissura hippocampi, or misapplied expression fissura dentata, I do not suggest any alteration in the terms now in use, nor any application of these terms in a manner which has not been already adopted by certain anatomists.

As our knowledge of the structure of the body becomes more exact, it is necessary that terms used at first in a vague manner should be exactly defined. It is time for the brain to be treated with the same respect as has been long shown to other parts of the body. Hitherto anatomists have felt that, since so little is known with regard to the specialization of its functions, the accurate delimitation of its regions is of little moment.

SUMMARY OF CONCLUSIONS.

In Chief.—1. The fascia dentata is absent from the brains of *Hyperoodon rostratus* and *Monodon monocerus*. It is but very slightly developed in *Phocæna communis*. In *Phoca vitulina* its size is small.

2. The extension of the fascia dentata in the several members of the Mammalian class varies as the relative development of their olfactory apparatus.

Subsidiary.—*a.* The column of large cells known as the nucleus fasciæ dentatæ is the extreme margin of the general cortex.

b. The granular and molecular layers of the fascia dentata belong to a separate portion of the wall of the fore-brain which has undergone this characteristic development.

c. In osmatic brains the fascia dentata ends on the mesial surface of the brain, slightly in front of the anterior end of the ventricular slit. Towards its anterior extremity its mesial and external portions or limbs meet below in an acute angle. At its extreme anterior end the two limbs of the V are opened out into a flat band which lies on the surface.

d. At its posterior or upper end the fascia dentata terminates abruptly. It is therefore a long riband, folded into a trough; if laid out flat, the riband would be found to have a nearly uniform width and a very regular and uniform structure.

e. Excluding neurogleial cells, blood vessels, and occasional large pyramids, the stratum granulosum of osmatic brains contains two kinds of cell: (1) "granules," (2) small pyramids. In a typical section from the brain of the Ox I find an average of one pyramid to eight granules.

f. The anterior commissure and the fornix vary in thickness as the relative development of the rhinencephalon, although neither of these structures is absent from anosmatic brains. In anosmatic brains the posterior pillars of the fornix are closely adherent to the under surface of the corpus callosum.

g. There is no reason for associating the fascia dentata with the striæ longitudinales (nervus Lancisii), gyrus supracallosalis, and gyrus geniculi, or for supposing that all these four structures belong to a single organ, which forms a part of the cortical centre for the sense of smell. The fascia dentata is a subcallosal structure; it alone disappears in completely anosmatic animals. The stria longitudinalis lateralis and the minute convolutions (supracallosal and geniculate) into which it enlarges anteriorly are found in animals destitute of olfactory bulb or tract.

h. The relative representation of olfaction in brains of different species is shown by the ratio which the length of the hemisphere bears to its other dimensions.

DESCRIPTION OF PLATES.

PLATE 23.

Fig. 1. A portion of the fascia dentata from the anterior end of the hippocampus of the Calf. *Magnified* 500 *diameters.*

It consists of some granules with nuclei which stain darkly, and others with nuclei which do not stain; several of the latter are in process of division. Small pyramidal cells are also seen amongst the pyramids. The grey matter exhibits a delicate fibrillation. It contains sparse nerve-cells.

The blood corpuscles are stained darkly; they lie in chains in the capillary vessels.

Fig. 2. The hippocampus of *Hyperoodon rostratus.* Section 4B. Stained with carmine-alum, followed by hæmatoxylin after WEIGERT's method, slightly modified.

The fimbria is seen as two ridges, from the larger of which springs the ependymal wall of the ventricle.

The cortex almost reaches the surface, where it ends with a blunt border. A blood-vessel is cut across at the edge of the cortex, and beneath this a few small pyramidal cells, which represent the fascia dentata, descend on the surface of the molecular layer of the gyrus uncinatus.

Fig. 3. Hippocampus of a young Narwhal (*Monodon monoceros*). Section 6B. *Magnified* 9 *diameters.*

This section was carried through the region in which the traces of hippocampal formation are more distinct than in any other part.

O.T., optic tract; *T.S.*, tænia semicircularis; *N.W.*, basal optic nucleus of WAGNER; *E.W.*, ependymal wall of descending horn of the lateral ventricle; *V.I.*, velum interpositum; *F.*, fimbria; *H.*, reflection of the cortex at the hippocampus; *G.H.*, gyrus hippocampi (*seu* uncinatus); *A.G.*, groove for an artery.

PLATE 24.

Fig. 4. Right hemisphere of the brain of the Porpoise (*Phocæna communis*) from the basal surface, to show the uncinate convolution (natiform protuberance,

&c.). The base of the 'tween-brain was injured, and hence details in its structure are not shown.

Fig. 5. Hippocampal region of the Porpoise. *Magnified* $\frac{3}{2}$.

A. As seen from the (mesial) surface.

B. As seen from the lateral ventricle.

C. As seen from behind and mesially.

Fig. 6. Five blocks cut from the hippocampal region of the Porpoise brain. Each of the blocks is drawn as it appears from the front, the four intervening blocks being omitted. *Magnified* $\frac{5}{2}$.

The sections exhibit the want of development of the reflected portion of the cortex.

C.A., the most posterior block, shows the strap-shaped posterior pillar of the fornix as it appears where it first touches the cortex of the uncinate gyrus. *P.p.f.*, posterior pillar of the fornix ; *Ch.pl.*, choroid plexus, collected into a mass.

6C and 6D, the fimbria, *fi.*, reduced to small dimensions, rests on the apex of the reflected portion of the cortex.

6E is carried through the nucleus amygdaleus, in front of the anterior end of the hippocampus.

Fig. 7. A semi-diagrammatic view of a section (3B) of the hippocampus of *Hyperoodon rostratus*, near its anterior end ; showing the double curvature of the cortex and the looped layer of minute scattered cells which occupies the place of the fascia dentata.

E., ependymal wall of the descending horn of the lateral ventricle; *V.* III., lateral ventricle ; *F.D.*, vestige of fascia dentata ; *G.H.*, gyrus hippocampi, *seu* uncinatus ; *F.C.*, fissura collateralis.

PLATE 25.

Fig. 8. Photo-lithograph of a cast of the interior of the skull of *Hyperoodon rostratus;* showing the conical form of brain which is characteristic of anosmatic animals. *One-third natural size.*

Fig. 9. Photo-lithograph of a cast of the interior of the skull of a young Porpoise. *Two-thirds natural size.*

Fig. 10. Transverse section through the hippocampus of a Porpoise. Section 9A, taken from rather behind the middle of the region.

Ch.Pl., choroid plexus ; *F.*, fimbria ; *R.C.*, reflected cortex.

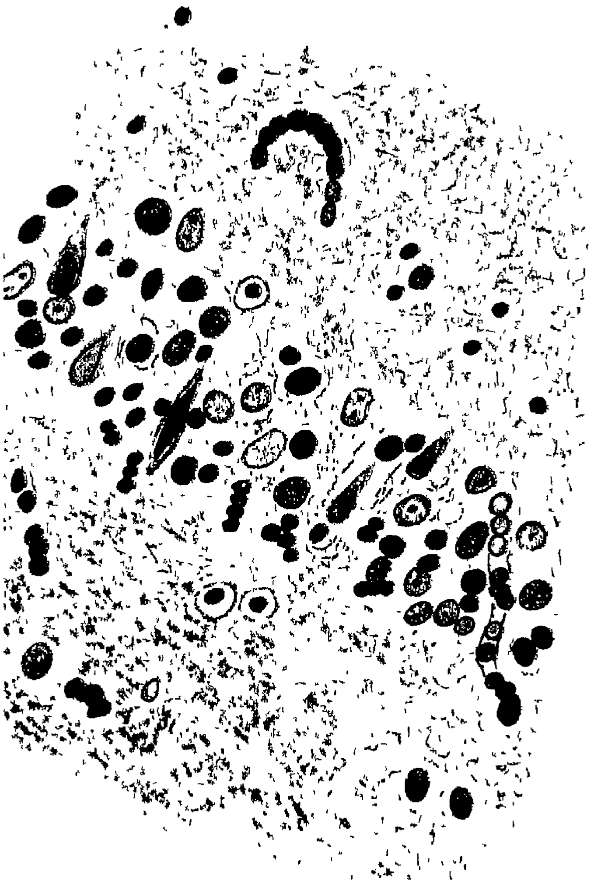
Fig. 11. Transverse section through the hippocampus of a Porpoise. Section 5A,

carried through the very limited region in which the reflected cortex appears on the surface, enclosed in a sheath of fascia dentata.

Fig. 12. The under surface of the brain of *Monodon monoceros* (fœtus at full term), as it is seen after removal of the hind brain, by a transverse section through the front of the pons Varolii. The drawing shows the extent to which the brain is folded upon itself.

O.ch., optic chiasm; *C.C.*, crus cerebri; *F.*, fillet; *P.C.Q.*, posterior tubercle of the corpora quadrigemina; *A. C.Q.*, anterior tubercle; *U.*, uncus, completely separated from *G.U.*, gyrus uncinatus *seu* hippocampi; *Sp.C.C.*, splenium corporis callosi.

Fig. 13. Transverse section of the hippocampus of a young seal (*Phoca vitulina*). Section 4B, carried through the region in which the hippocampus is best developed. The fascia dentata is seen lying at the bottom of the dentary fissure.



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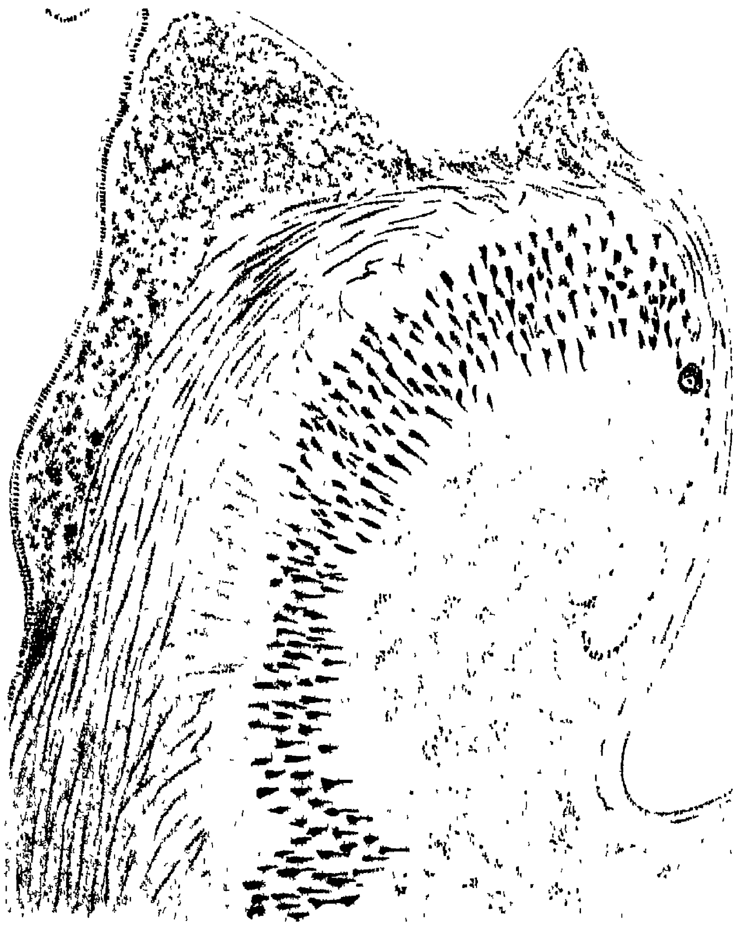

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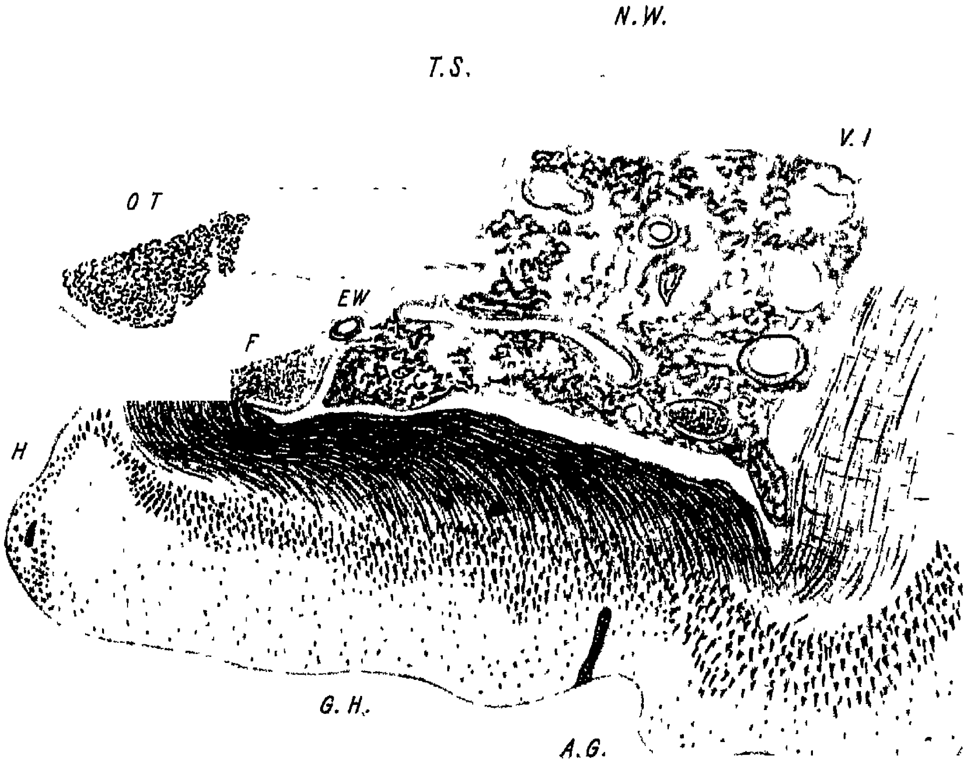

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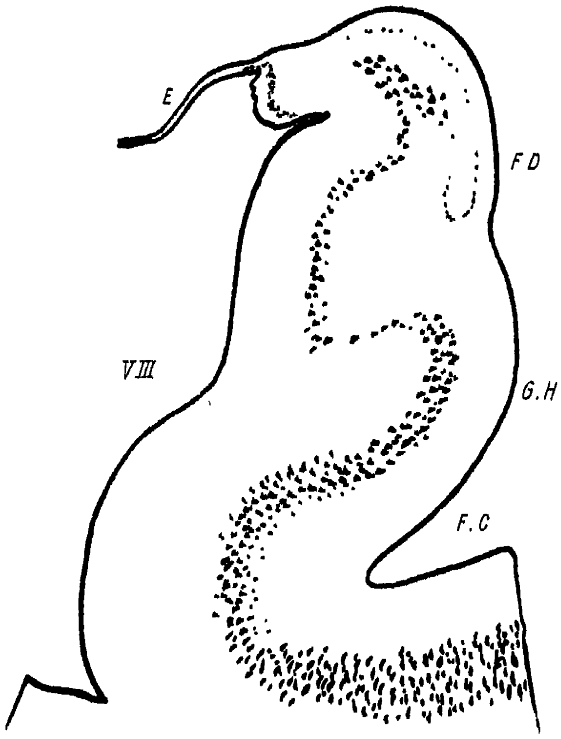

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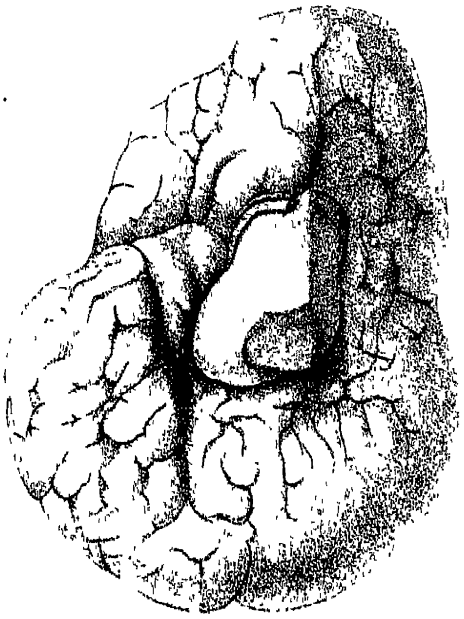

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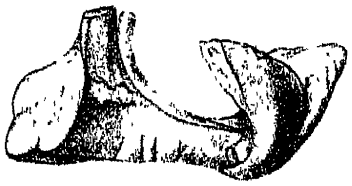

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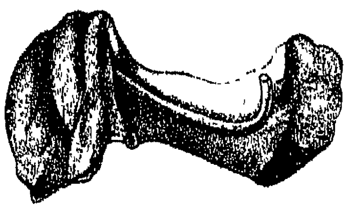

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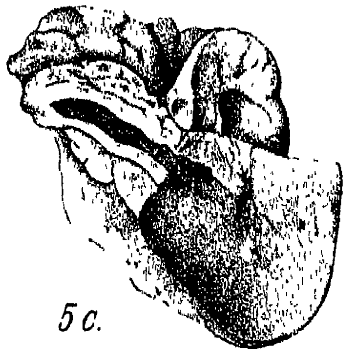

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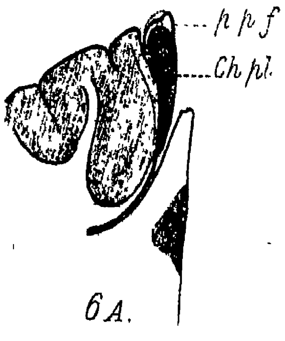

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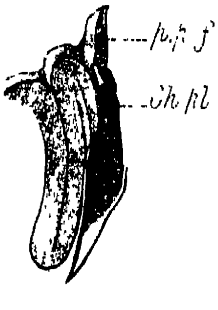

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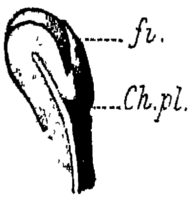

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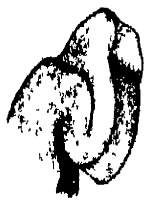

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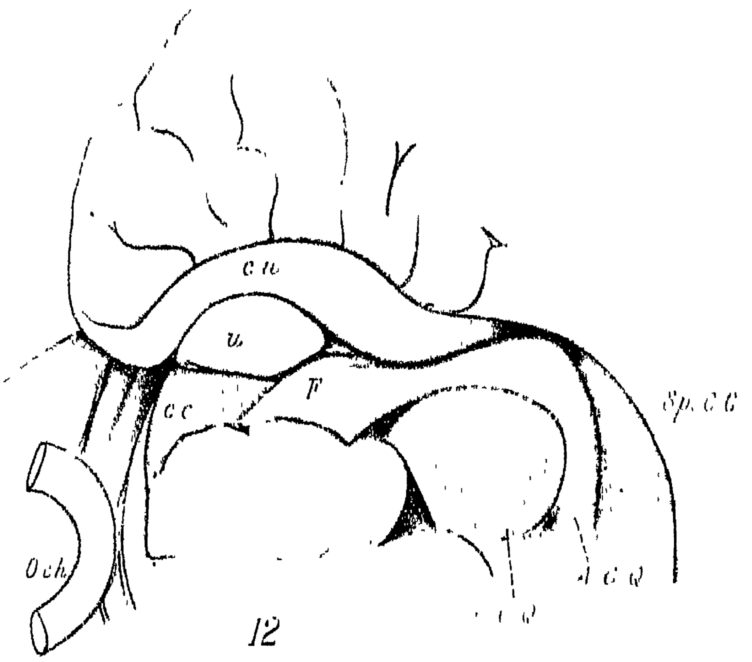

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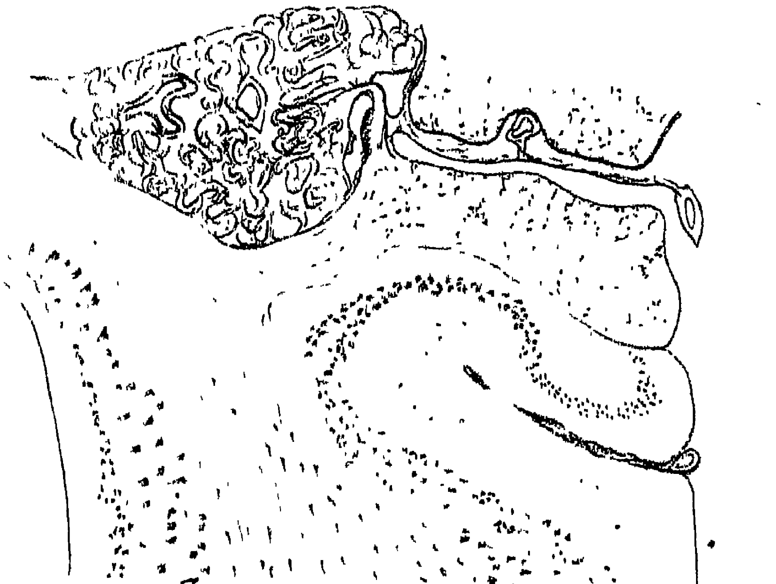

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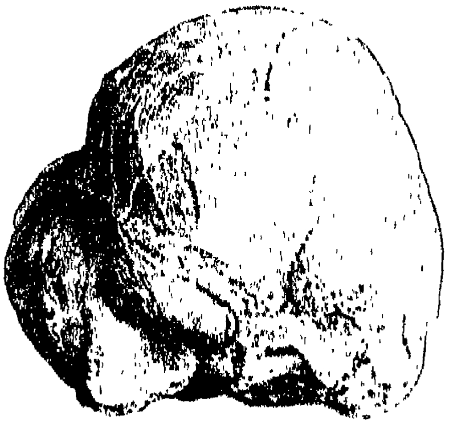

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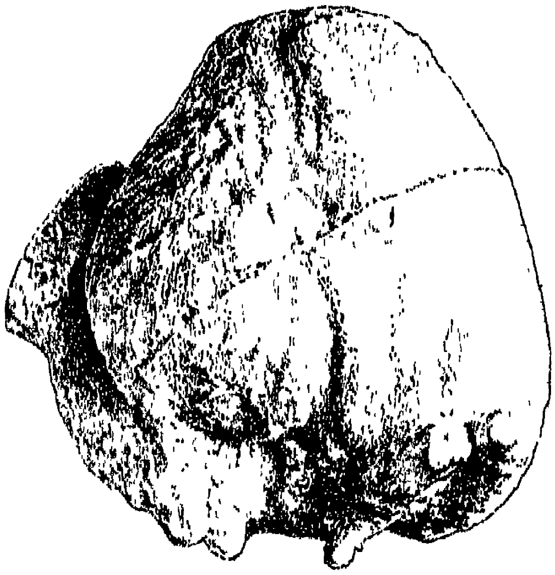

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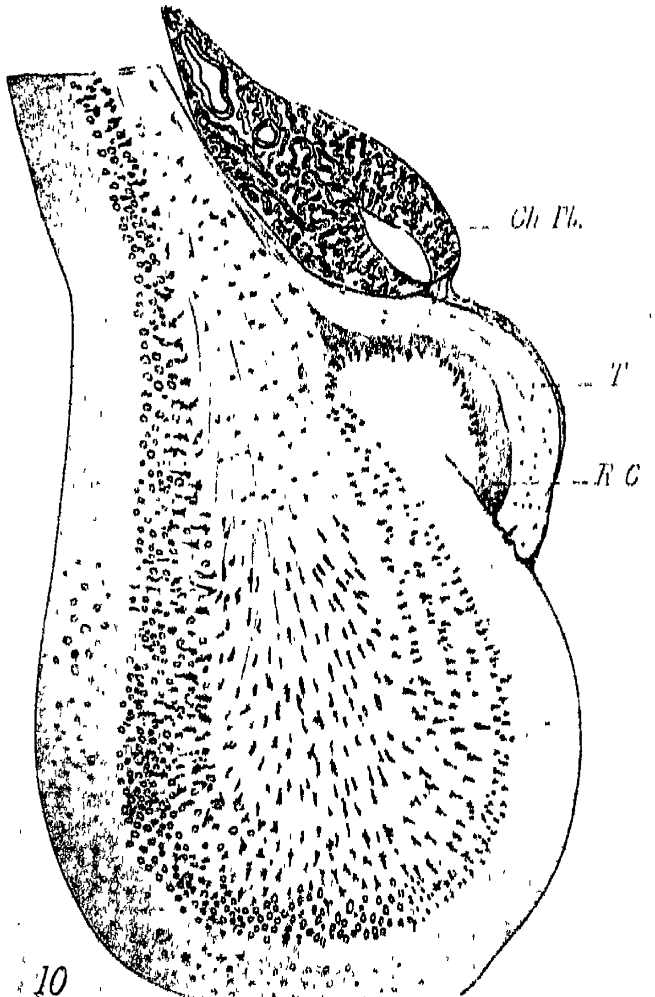

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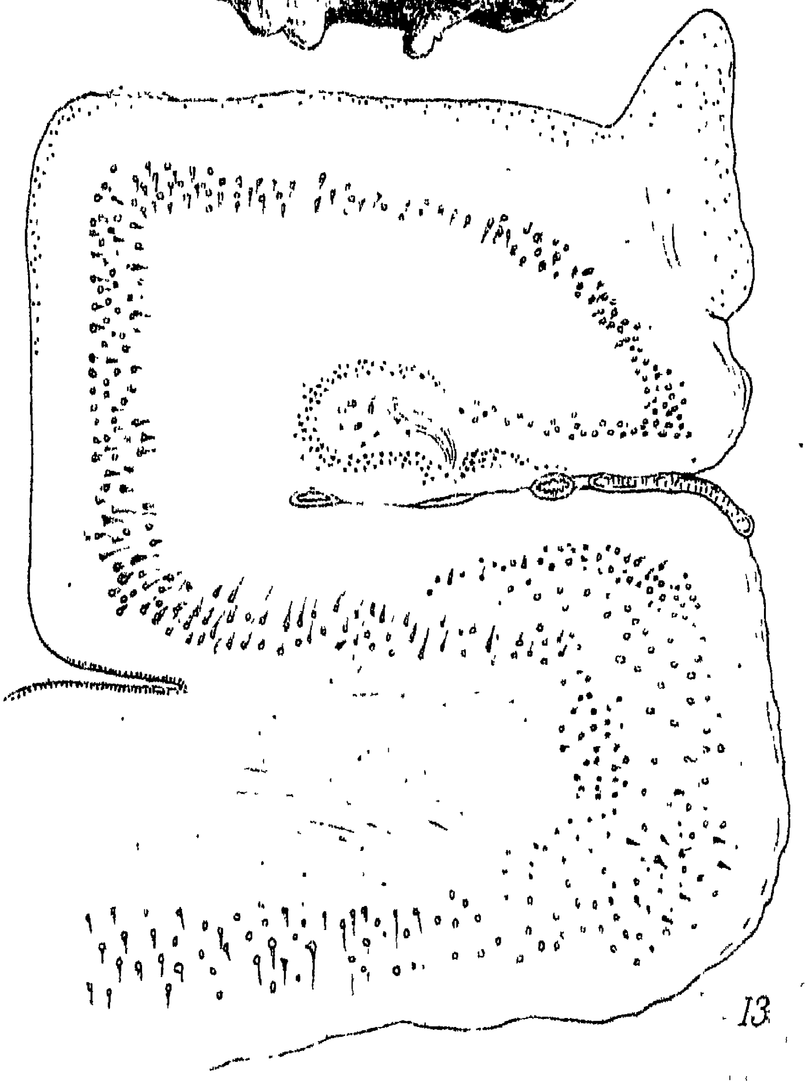

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VII. *On some New Reptiles from the Elgin Sandstones.*

By E. T. NEWTON, *F.G.S., F.Z.S.*

Communicated by Sir ARCHIBALD GEIKIE, *For. Sec. R.S.*

Received November 28,—Read December 15, 1892.

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I.—INTRODUCTION.

THE earliest discovery of Reptilian remains in the Elgin Sandstone, was made by Mr. A. ROBERTSON, at Lossiemouth. The specimens consisted of a series of scutes, drawings of which were submitted to M. L. AGASSIZ, who, believing them to be of

Old Red Sandstone age, described them in 1844 (1*) as scales of a Ganoid Fish, which he named *Stagonolepis Robertsoni*.

In the year 1850 Captain LAMBART BRICKENDEN found some quadrupedal footprints at Cummingstone, in beds of the same age as those at Lossiemouth, which he described (5), and at the same time gave an account of these so-called Old Red Sandstone rocks. He also mentioned the discovery, by Mr. PATRICK DUFF, of a small Reptile at Spynie. This specimen was described in detail by Dr. G. A. MANTELL (26) in a paper immediately following that by Captain BRICKENDEN, as a small Lizard with certain Batrachian affinities.

In 1858, Sir R. I. MURCHISON (27) read a paper on the relations of the Elgin Sandstones, and concluded that they could not be separated from the Old Red Sandstone, but must be regarded as forming the upper part of the series. In a note to this paper (27, p. 434) Sir RODERICK quotes Mr. PATRICK DUFF's short historical sketch of these early discoveries in the Elgin Sandstone, and then mentions in a postscript the finding of another fossil by the Rev. G. GORDON "in the same beds at Lossiemouth, in which *Stagonolepis* occurs," and says "Professor HUXLEY terms this new Reptile *Hyperodapedon Gordoni*."

The Right Hon. Professor HUXLEY (12), in a paper following that by Sir RODERICK MURCHISON, described bones, teeth, and scutes which had been found at Lossiemouth and Findrassie, referring them to *Stagonolepis*; but showing that they belonged to a Crocodilian Reptile and not to a Fish as had previously been supposed. Among these remains was a portion of a jaw with four large teeth, the largest of which projected 2¼ inches beyond the alveolar margin. Although including this jaw provisionally with *Stagonolepis*, the Professor says, "there is no positive proof that this fragment of a jaw belonged to *Stagonolepis*;" and in his later Memoir in 1877 (18), the teeth of *Stagonolepis* having been found, this jaw, although of uncertain affinities, was called *Dasygnathus longidens*.

At p. 460 of the earlier paper (12) *Hyperodapedon* is alluded to, and then follows this noteworthy sentence, "its marked affinity with certain Triassic Reptiles, when taken together with the resemblance of *Stagonolepis* to Mesozoic Crocodilia, leads one to require the strongest stratigraphical proof before admitting the palæozoic age of the beds in which it occurs."

In the year 1866 Professor HUXLEY (14) described a new example of *Telerpeton Elginense* from Lossiemouth, which included the skull, lower jaw, vertebral column and ribs, with both pectoral and pelvic arches. In the concluding part of this paper (p. 83), the following conclusions are given. "From the description of the organization of *Telerpeton Elginense* which has now been given, it is obvious that this animal is one of the Reptilia, devoid of the slightest indication of affinity with *Amphibia*. It is Saurian in all its characters, . . . and must be referred to the true *Lacertilia*."

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[*] The numbers refer to the list of works, p. 495.

Sir RODERICK MURCHISON in 1867 (28), having heard from Professor HUXLEY of the discovery of *Hyperodapedon* in the Trias of Warwickshire (see 15), said, "To such fossil evidence as this, the field-geologist must bow; and instead, therefore, of any longer connecting these reptiliferous sandstones of Elgin and Ross with the Old Red Sandstones beneath them, I willingly adopt the view established by such fossil evidence, and consider that these overlying sandstones and limestones are of Upper Triassic age."

In 1869 Professor HUXLEY (15), described the remains of *Hyperodapedon* from Lossiemouth, to which he had alluded in his paper on *Stagonolepis* in 1858 (12, p. 460), as well as other specimens afterwards received from the same neighbourhood. In addition to these were noticed jaws with teeth referable to the same genus, if not to the same species, which had been found in the undoubted Triassic Sandstone of Coton End, Warwickshire; also a jaw from beds of similar age near High Peak, South Devon; and a number from the Maledi (Trias) beds of Central India, some of which had been presented to the Geological Society in the year 1860. The Indian forms have since been described by Mr. R. LYDEKKER (22).

In 1875 Professor HUXLEY (17) gave a further account of *Stagonolepis*, based on numerous remains from the Elgin Sandstone, which had from time to time been forwarded to him by Dr. GORDON and Mr. GRANT; but these were more fully described in the Geological Survey Memoir which appeared in 1877 (18). In the introductory remarks to this Memoir a short history of these discoveries is given, and at p. 43, the Professor refers to the jaw provisionally referred to *Stagonolepis*, and places it in a new genus and species, *Dasygnathus longidens*. At the end of this Memoir the Rev. Dr. GORDON gives a note on the geological structure of the Elgin district, accompanied by a sketch map.

Mr. J. G. PHILLIPS, in 1885, at the British Association Meeting (40), gave some account of the Elgin Sandstones, and pointed out that, at Cuttie's Hillock Quarry, near Elgin, *Holoptychius* had been found in the lower part, and Reptile remains in the upper part, of what did not appear to him a quite conformable series of deposits; and he thought that the true relations of these beds had not been definitely settled.

Dr. R. H. TRAQUAIR (45), in the same volume of the 'British Association Reports,' in a "Preliminary Report on a New Fossil Reptile recently discovered at New Spynie, near Elgin" [now known as Cuttie's Hillock Quarry], says the presence of a large tusk immediately behind the premaxillary region, and the whole appearance of the skull, indicate a Reptile belonging to the group of the Dicynodontia.

Professor JUDD, in the latter part of 1885 (20), read a paper before the Royal Society, "On the Relation of the Reptiliferous Sandstone of Elgin to the Upper Old Red Sandstone," in which he gives an account of the discoveries of Reptile remains in these Elgin Sandstones, and mentions two specimens obtained near Elgin [Cuttie's Hillock]; one of these was at first thought to show Dinosaurian characters, but this has not been confirmed; while the other exhibited the characteristic features of *Dicynodon*

—it is, in fact, the specimen noticed by Dr. TRAQUAIR (45), and belongs to the Geological Survey. The more important point in Professor JUDD's paper is the description of the section at Cuttie's Hillock Quarry (also known as New Spynie), in which, as he believes, the reptiliferous beds rest unconformably upon Old Red Sandstone, the junction being marked by a bed of conglomerate, called by the workmen "pebbly post." The Geological Survey, however, has failed to trace this unconformability.

In 1887, "Further Observations upon *Hyperodapedon Gordoni*" were made by Professor HUXLEY (19), when he described in detail a fine specimen of this Lizard from Lossiemouth, which had been secured for the British Museum. In this paper the affinities of *Hyperodapedon* are discussed, and its close relationship to *Sphenodon* fully established.

Within the last few years the Elgin Museum has obtained several specimens of Reptilian remains from the Elgin Sandstone of Cuttie's Hillock, and, through the courtesy of the Directors of that Institution, and the kind intervention of the veteran geologist, the Rev. Dr. G. GORDON, they have been sent to the Geological Survey in London for examination and description. Three other examples from the same horizon and locality are in the possession of the Geological Survey.

My colleague, Mr. J. HORNE, pointed out the desirability of these specimens being definitely determined, and, at the desire of Sir ARCHIBALD GEIKIE, the Director-General of the Geological Survey, I undertook the task of working out these fossil remains. The results of this investigation form the subject of the present communication.

When the specimens from the Elgin Museum first reached me they did not promise very satisfactory returns for the labour of developing them, although it was evident that they belonged to forms which had not before been described. They were still in the condition in which they had come from the quarry, except that some had the faces much rubbed; and the edges of the cavities, for they were all in the condition of hollow moulds, had lost their sharpness. Each example, with one or two exceptions, was in several pieces, and had to be fitted together before the task of developing it could be commenced. When the Survey specimens came into my hands they were in a similar state to those belonging to the Elgin Museum, but the skulls were in a much more promising condition, and supplied information which was not obtainable from the others.

The reptiliferous sandstone from Cuttie's Hillock Quarry is variable in texture, most of the specimens being coarser than those from Lossiemouth, which contain the remains of the *Stagonolepis*, described by Professor HUXLEY in 1875 (17), and consequently it is not so satisfactory for the preservation of the imbedded bones. Like many of the *Stagonolepis* remains, these Cuttie's Hillock specimens have not a particle of the bones left, the whole having been dissolved, leaving merely the cavities where the bones have been. The surfaces of these cavities are stained more or less with iron, and are thus a little darker than the surrounding matrix; they are also frequently marked with black spots and patches, which are sometimes sufficiently thick to allow of pieces being removed with a penknife. My colleague, Mr. G. BARROW, has been good enough to analyse some of this black substance, and finds it to contain iron, manganese, and a trace of cobalt. In some instances the cavities have been partly refilled by fine sand and oxide of iron; in others, their sides have been pressed together and the space nearly obliterated; while some are distorted by pressure, apparently before the dissolution of the bones. It will readily be understood that the task of developing these fossils was by no means an easy one; and indeed great caution had to be used to prevent some of the parts being broken away without being seen. In many cases the cavities differed so little in colour from the surrounding matrix, and were so easily obliterated, both by bleaching and by the crumbling of the surface, that it became necessary to find some means of preserving them as soon as possible after being exposed. For this purpose shellac varnish was used, which had the effect of hardening the stone and deepening the colour. In working out the specimens, the impressions which had been exposed by the splitting open of the block were in the first place varnished, and, when dry, wherever a cavity could be seen passing under the stone it was carefully followed, little by little, with small chisels, one side of the cavity being removed, and the newly-exposed parts varnished. In many cases it was found possible to split open the cavities, thus exposing and preserving the impressions of both sides of the bone. The surrounding matrix was subsequently treated with gelatine. From the specimens thus prepared, casts in gutta-percha were taken, which reproduced the forms of the original bones. In many instances, more especially in the case of the skulls, separate casts of the various parts had to be taken, and afterwards fitted together. The interpretation of many of the bones would have been almost impossible without such casts, which, it must be remembered, are not merely *models* of the specimens, which would be untrustworthy, but they represent the original bones, like any fossils in which the bone has been replaced by another substance.

The specimens described in this communication are all new to science, and are from the Elgin Sandstone of the one locality known as Cuttie's Hillock Quarry, which has sometimes been called "New Spynie," and they represent, at least, eight distinct skeletons. Three of these belong to the Geological Survey, and the remainder to the Elgin Museum. Seven of the specimens are undoubtedly referable to the Dicynodontia; some being closely allied to the type genus *Dicynodon*, and one nearly related to *Ptychognathus*, while another, having the skull ornamented with many horns, is one of the most extraordinary fossil animals that has come to light for many years, and this seems most nearly related to *Pareiasaurus*.

In the working out of these specimens I have received assistance from many kind friends, and take this opportunity of acknowledging my indebtedness to them. In the first place I am under obligation to the Rev. Dr. GORDON, of Elgin, whose enthusiasm has been the means of rescuing many of the specimens, and who has spared no trouble to send several hundredweights of stone to London for my examination.

The officers of the British Museum have, with their usual courtesy, afforded me every facility for the study of the fossils under their charge. To my friends, Professor G. B. Howes and Mr. R. Lydekker, as well as to my colleagues, Mr. G. Barrow, Mr. F. W. Rudler, Mr. W. Topley, and Mr. H. B. Woodward, I am indebted for many useful suggestions and valued aid afforded in the course of the work. I am also under obligation to my colleagues, Mr. J. J. H. Teall and Mr. H. A. Allen, for the trouble they have taken in photographing some of the specimens; to Mr. W. M. Redaway for his careful drawings made from the casts; and to Mr. A. T. Hollick for his successful delineation of them on stone.

II.—DESCRIPTION OF SPECIMENS

A. DICYNODONTIA.

Gordonia, *gen. nov.*

1. Gordonia Traquairi, *sp. nov.* (Plates 26 to 28.)

General Remarks.

It is one of the specimens belonging to the Geological Survey that will be first noticed, as it supplies more information concerning the structure of the skull than either of the others, and will be convenient as a standard for comparison. This is the specimen referred to by Dr. Traquair (45) in 1885 as belonging to the Dicynodontia, and it was hoped that a detailed description of it from the pen of so able a palæontologist would, ere this, have been published; unfortunately, however, official duties have prevented his devoting his attention to these interesting remains.

I had already developed and described the remains included in the first consignment of the Elgin Museum specimens, when Sir Archibald Geikie desired me to include with them the description of the Survey examples, at that time in Edinburgh, which proved to be of great service in clearing up certain difficulties, more especially in the interpretation of parts of the skull.

The specimen now to be described (Plate 26) is contained in three slabs of sandstone, and includes, besides the skull, fragments of several ribs, parts of a scapula, and of a humerus, with possibly parts of two or three caudal vertebræ. In common with all the other remains noticed in this paper, the bones are only represented by cavities in the stone, which, having been laid open in the manner above explained, casts have been made, from which the descriptions are for the most part taken.

Description.

Skull.—The skull has been, most fortunately, split vertically from front to back, nearly in the middle line, so that the left half (Plate 26, fig. 2), after clearing away some of the matrix, has allowed a cast to be made representing an entire side of the skull and lower jaw (Plate 27), and the same cast, with a few particulars obtained from the right side, gives the form of the upper surface (Plate 28, fig. 1). The right half of the skull supplies details for the reconstruction of the palate and other central parts (Plate 28, fig. 2).

Although some of the bones have been cracked and broken, the parts are very slightly, if at all, displaced, and the general contour of the skull has suffered very little alteration. The greatest length of the skull (Plate 27) from the premaxillary region to the back of the squamosal is 185 millims.; while its height from the quadrate condyle (*qu.*) to the parieto-squamosal crest (*pa.sq.*) is nearly 110 millims. The greatest width, across the temporal bars (Plate 28, fig. 1), cannot be absolutely measured, but must have been about 110 millims., or perhaps a little more. The most striking features of the skull (Plate 27), in addition to the characteristic tusk, are the great depth at the hinder part, due to the disproportionately large pedicle for the lower jaw, and the wide laterally-directed plate of the squamosal (Plate 28, fig. 1), forming the outer boundary of the temporal fossa, while the anterior part of the skull is much narrower.

Upper Surface of Skull.—Seen from above (Plate 28, fig. 1), the skull is regularly pear-shaped, the broad hinder half being formed by the temporal region, with its wide temporal bars, enclosing on each side a large supratemporal fossa, which is bounded anteriorly by the postorbital bar. The parietal region is narrow, a deep, longitudinal groove occupying the middle line, on each side of which is a prominent crest, that externally slopes downwards and outwards into the temporal fossa, the surface thus formed being concave above and convex lower down; it is narrow anteriorly but widens as it passes backwards. Each crest rises from the hinder margin of the postorbital bar and passes backwards and inwards, almost meeting its fellow of the opposite side, with which it runs nearly parallel for some distance, then diverging in the occipital region, it sweeps downwards, backwards, and outwards, meeting, at the hindermost extremity of the skull, the outer plate of the temporal bar, with which it is continuous. These crests occupy the parietal region, but do not seem to be formed by the parietal bones alone, for a depressed line, probably indicating a squamous suture, can be traced along their upper and inner edges, the inner lamina apparently belonging to the spindle-shaped area (Plate 28, fig. 1) which encloses the pineal fossa. This suture is best seen in a cast taken from the right half of the specimen. According to Professor SEELEY (43) these temporal plates in *Dicynodon* appear to be formed by bones which overlie the true parietals and are continuous with the squamosals; and certainly in the Elgin specimen there is no sign of any divisional suture between this plate and the squamosal; it appears therefore that the last-named bone, besides forming the greater part of the temporal bar, extends along the upper border of the temporal fossa, forming the outer plate of the crest; moreover, it appears to extend downwards on the outer side of the quadrate, leaving only a small part of the latter exposed on the outer surface. A line which is seen crossing the quadrate just above the articular condyle (Plate 27, *qu.*) may perhaps mark the lower end of the squamosal.

Between the anterior part of the parietal crests (Plate 28, fig. 1) is the large oval pineal fossa, which, as can be seen in the right half of the skull (Plate 28, *pn.*), forms a very distinct cup, opening below into the brain cavity. The deep cup-like form of the pineal fossa is probably an indication that it lodged a well-developed eye.

The pineal fossa is situated in the hinder half of a spindle-shaped area, marked off by sutures, which is anteriorly in relation to the frontals, and posteriorly is wedged in between the parietal crests. This area seems to correspond with the similarly shaped parietal bones of *Sphenodon*, which likewise enclose the pineal fossa. In the present specimen this spindle-shaped area is not formed by the parietals alone, for a little behind the anterior margin of the fossa a suture passes inwards from each side, thus separating the spindle into an anterior triangular bone, forming the front boundary of the pineal fossa and wedged in between the hinder ends of the frontals, and a posterior triangular area enclosing the greater part of the pineal fossa. The hinder part of the spindle is so shut in by the crests in this skull that its structure cannot be well seen; but in specimen No. 3 (Plate 32, fig. 2), which has a larger spindle, a suture is clearly seen passing backwards from the fossa and dividing the hinder triangle into two portions; this suture doubtless existed in the present specimen. The portion of a Dicynodont skull from India, described by Professor HUXLEY (15, p. 10), Plate 30, fig. 1, presents a very similar structure of this area, and he regards the two bones forming the hinder half of the area as the parietals, and the anterior one as an intercalary bone. Professor COPE (8, p. 210) notices the same posterior median suture in his *Lystrosaurus*, but judging from his figure the pineal fossa is entirely surrounded by the two anteriorly connate parietals.

The upper surface of the skull (Plate 28, fig. 1) immediately in front of the pineal fossa, and between the postorbital bars, is deeply depressed, and in the middle of this depression is a smaller concavity occupying the anterior part of the spindle-shaped area; extending forwards from this is a median ridge, apparently co-extensive with the frontals which occupy the inter-orbital space and seemingly meet the premaxillæ some little distance in front of the orbits, a deep transverse pit marking the point of junction. The frontal suture is seen as a line running along the median ridge. The form of the front of the muzzle is somewhat uncertain; the figures, however, fairly represent its present condition, that is notched at the extremity, but this appearance may, to some extent, be due to imperfection. The premaxillæ no doubt form the anterior extremity, and extending downwards in the middle line (Plate 27), divide the anterior nares, which are double and lateral, though very near to the front and to each other.

On the outer side of the frontal process of the premaxilla and extending from the frontal to the anterior nares, is an elongated bone which occupies the position of the nasal. At its hinder end and separating it from the orbit, is a small triangular area which I regard as the prefrontal; this bone forms part of the orbit (Plate 27), and is in relation with the frontal, nasal, and lachrymal bones, the latter being best seen in the side view which we come next to consider. Each of the bones of the front of the skull occupies the same relative position as those described in Dicynodonts by Professors COPE (8) and SEELEY (43), but in the restored plan given by the latter (p. 247) the nasals are not indicated.

Side View of Skull.—The premaxilla, as seen in a side view (Plate 27) forms in front of the nasal opening a peculiar beak-like projection, which may, perhaps, be due to fracture; but is not unlike what is seen in *Dicynodon pardiceps* of OWEN (38, Plate 38). No suture is to be seen between the premaxilla and the maxilla, but it is the latter undoubtedly which carries the tusk and hides the greater part of it, only about 10 millims. being seen projecting downwards, forwards, and inwards, beyond the alveolus; and when perfect, scarcely 5 millims. could have been exposed. The length of this tusk must have been about 50 millims., and its greatest diameter, perhaps, 10 millims. The distance between the points of the two tusks seems to have been about 35 millims., but the right tooth is not seen.

Each nasal opening is directed laterally, and while its anterior border is well defined and stands out sharply, the posterior edge is ill defined, the bone being depressed and shelving inwards and forwards; indeed the true opening is not so large as it appears to be in the outer view (Plate 27), where the matrix obscures the hinder margin. The true opening, as shown on the opposite block of stone, is smaller and is indicated by a line in the figure.

The orbit is large and oval, measuring from front to back 45 millims., and in height 35 millims.; it is directed outwards, forwards, and a little upwards, its lower and hinder boundaries are narrow bars, showing no sutures to indicate the limits of the bones; but judging from the structure in other Dicynodonts, the postfrontals form the postorbital bar, and the jugal bone, in part at least, the lower bar. If the structure indicated by Professor SEELEY holds good in this specimen, the maxilla underlies the jugal and unites with the squamosal for some distance in the temporal region, thus helping to form the temporal bar. A suture is to be seen on the under surface of the temporal bar (Plate 28, fig. 2), but there is nothing to show whether the bone in front of it is part of the maxilla or part of the jugal. The orbit is continuous, below and behind, with the great temporo-palatine vacuity.

Within the front of the orbit is the lachrymal foramen, which passes through into the nasal chamber and may be seen on the inner surface. The sutural boundaries of the lachrymal bone are not very clear, but they may be traced within the orbit and on the outer surface extending from the orbit to the nasal aperture. Immediately above the lachrymal is the triangular bone above called the prefrontal.

The parieto-squamosal crest arises abruptly behind and above the orbit, increasing in height as it passes backwards, and then curving downwards sweeps backwards and outwards to meet the temporal bar. As we have already seen, the outer plate of the crest seems to be formed by the squamosal, which apparently also includes the downward extension forming the pedicle for the lower jaw. The pedicle has a remarkable form; as it descends from the temporal bar it has a broad surface (45 millims.) directed outwards, which is convex from before backwards; it is then twisted so as to turn the outward face nearly forward, and becomes concave from side to side; its outer margin forms an angle and then curves downwards, inwards, and forwards to the quadrate; the lower end is much constricted and again twisted so that the front face becomes once more directed outwards, a line near the condyle being possibly the suture between the squamosal and the quadrate.

Passing from the inner side of the quadrate, the outer edge of the pterygoid is seen stretching forward to join the maxilla below the orbit; but the form of the palate is hidden in this side view.

Palate.—By clearing away the matrix from above the palatal region of the right half of the skull it has been possible to obtain casts representing the greater part of the palate, and from these, with a partial restoration, the drawing (Plate 28, fig. 2) has been made. The base of the cranium being hidden, its relation to the pterygoids is uncertain, but it is tolerably clear that the united pterygoids were continuous with the basisphenoidal region. The under surface of the palate is concave from side to side throughout its length, but especially so at the extremities; while from front to back along the middle it is convex, a ridge, carrying a suture, occupying the middle line. A strong process is given off from the hinder part of the pterygoids on each side, which passing downwards and backwards joins the inner side of the quadrate well above the articular condyle (Plate 28, fig. 2, *qu.pt.*) as seen also in a side view (Plate 27), thus giving a triradiate character to the hinder end of the palate. Immediately within the bases of these processes, and close to the middle line, is a pair of small holes piercing the pterygoids vertically. About 15 millims. in front of these foramina is the narrowest part of the palate, which widens again more gradually in front of this point. About 30 millims. in front of the pair of foramina there is a median ovoid aperture (*pt.f.*), pointed in front, which passes through the palate and opens into the supra-palatine vacuity, just behind the orbits. This opening, although single on the lower surface of the palate, is double above, being divided by a median ridge or septum, which, although not very clearly seen in this specimen, is much more distinct in the one next to be described (No. 2). Passing forwards from the narrowest part of the pterygoids their outer margins extend downwards and outwards, while the middle part inclines upwards, thus forming a deep wide channel between nearly vertical lateral plates. The outer surfaces of these lateral plates seem to be extensions of the pterygoids which join the maxillæ in front; but about the middle of the oval foramen (*pt.f.*) a suture is seen on each side curving outwards and then forwards, near the lower edge of this plate. The bone thus separated off on each side within the pterygoid is doubtless the palatine, it appears to join the maxilla, and then to turn inwards again. Although this region is obscured in the present specimen, yet, judging from others as well, there can be little doubt that the palatines extend to the middle line, either meeting each other, or being merely separated by the vomer, and thus form the posterior nares (*pt.na.*); these two passages passing directly upwards and forwards into the nasal chambers, are separated by the ethmovomerine septum, the hinder end of which can be traced, but its forward extension is hidden. Judging from the position of this septum in specimen No. 2, where it is well seen (Plate 29, fig. 2, *eth.vo.*), it would in the present specimen extend forward to a point between the external nares (Plate 27, *n.*).

The posterior nares being situated between the front parts of the orbits, the boundary of each nasal passage forms part of the wall of the orbit, and passes just on the inner side of the maxillary cavity, which contained the pulp of the tusk-like tooth. The upper surface of the pterygoid bones had a slight median ridge, but there is no evidence of an ossified interorbital septum. In clearing away the matrix from the interorbital region in the left half of the specimen, fragments of bone were met with, which seemed to correspond with a trough-like bone seen in the same region in specimen No. 2, which is believed to be an orbito-sphenoid.

The roof of the mouth in front of the posterior nares forms a deep concavity, extending so far upwards and forwards as to be in part between the external nasal openings, and it seems highly probable that it received a beak-like prominence of the mandible. The premaxillæ and maxillæ are doubtless the chief elements in the formation of this arched part of the roof of the mouth; but there is no evidence to show whether or not the vomer and palatines were included also.

Brain Case.—Little can be said as to the structure of the cranium proper, for the bones of this region are much broken; all the available information being in the right half of the specimen. The deep cup-like cavity for the pineal eye, already alluded to, is here seen very distinctly, and the manner in which it opens into the brain cavity by a narrowed foramen, which spreads out below into an inverted funnel-shaped space in the roof of the brain case, is also well shown. The pineal opening gives a clue to the position of the brain cavity which would otherwise have been uncertain, for although there are some thin plates of bone in this region, which are doubtless parts of the cranial walls, they are not sufficiently perfect to give any clear idea of the form of the brain case. Although only part of the roof of this cavity is seen, yet it is evident that it was nearly an inch below the highest part of the parietal crest, and that above the brain case there was a cavity on each side, continuous below with the temporal fossa, and covered above by the plates forming the parieto-squamosal crest.

Mandible.—The lower jaw is preserved *in situ* (Plates 26 and 27), and casts of both the inner and outer surfaces of the left ramus have been made; the bones, however, have been cracked and the limits of the different elements cannot be traced. The hinder extremity is shallow, and is close to the quadrate condyle. Passing forward its depth increases quickly for about one-fourth of its length, and then more gradually for about twice this distance, the anterior fourth maintaining the same depth to near the symphysis. The upper margin is convex in its present condition, but it seems probable that the anterior end was turned somewhat upwards to form a beak. The lower margin is concave from end to end, except where it is interrupted just behind the middle, by a broad thin process directed downwards and inwards. The ramus, as preserved, is nearly straight from back to front, but a little behind its anterior extremity, which seems to be its natural termination, the outer surface curves outwards forming a slight depression, possibly having some relation to the maxillary tusk. Both the inner and outer surfaces present a long oval vacuity at about the middle of their extent; that on the outside being bounded above by a strongly-marked ridge, which curves upwards towards the front. The greater part of the front half of the ramus is formed evidently by a dentary element, and its junction with the hinder half is shown at the upper margin by the two parts being drawn a little apart. A process from the hinder part of the ramus extends nearly to the front below the dentary.

A portion of the narrow symphysis is preserved in front showing that the two rami were perfectly anchylosed. The greatest length of the ramus is 105 millims.; its greatest depth, near the front, 40 millims., while towards the back, excluding the downward process, it is about 30 millims.

Parts of the Trunk.—The parts of the skeleton which are preserved, other than the skull, are in such a broken and fragmentary condition that they supply no satisfactory characters. A portion of what seems to have been a humerus, with the epicondylar foramen and bridge very strongly developed (Plate 28, figs. 3 and 4), gives no idea of the form of the entire bone, although it must have been more ponderous than any of the humeri described farther on.

A portion of a much broken flat bone, seen near the piece of humerus, is no doubt a scapula, probably similar in form to that of No. 2 specimen, and there are fragments of about a dozen ribs, the best exposed being about 9 millims. wide in the middle, and 13 millims. wide near the head. The ribs converge more or less towards the region which the vertebral column would naturally have occupied, but no traces of vertebræ are to be seen in this position. On the outer edge of the block, however, there are some indistinct impressions (Plate 28, fig. 5) which may have been left by three small elongated vertebræ; they are too indefinite to say much about, but their small size prevents their reference to any part of the body except the tail.

Affinities.

Dr. TRAQUAIR's reference of the specimen just described to the Dicynodontia (45) is fully justified by the detailed study of it now that it has been fully developed. The pair of maxillary tusks in the otherwise edentulous jaws, the large development of the pedicle for the articulation of the lower jaw, the double parieto-squamosal crest, sweeping round to the temporal arcade, and the structure of the palate, leave no room for questioning its close alliance with *Dicynodon*. Although the light build of the skull is quite unlike the ponderous proportions of most of the specimens that have been referred to that genus, yet it presents certain points of resemblance to both *Dicynodon* and *Oudenodon*, in its general outward appearance.

The genera into which Dicynodonts have been divided are not very clearly defined. The characters of the type genus *Dicynodon*, as given by Sir R. OWEN (38, p. 30) and modified by Mr. LYDEKKER (23, p. 1063), are tusk-like teeth in the maxilla growing from persistent pulps, the rest of the jaws being edentulous with trenchant edges. The profile of the skull rounded, the maxillæ not strongly ridged, nares approximated to the muzzle, and the supraoccipital forming a broad bar above the foramen magnum.

Oudenodon, OWEN, resembles *Dicynodon* in most points of its structure, but is distinguished by the total absence of teeth.

Kisticephalus, OWEN, was established for a number of small forms with depressed skulls especially broad in the inter-temporal region, and with no tusks. Mr. LYDEKKER (24, p. 47), however, has pointed out that teeth are sometimes present in this genus.

Ptychognathus, OWEN, has the skull strongly bent upon itself in front of the orbits, the maxillæ are strongly ridged and bear a pair of large tusks, the nasal openings are far from the muzzle.

Lystrosaurus, COPE, and *Dicynodon Murrayi*, HUXLEY, appear to be generically identical with *Ptychognathus*.

Keiroqnathus, SEELEY, was established for a small Dicynodont from South Africa and characterized as having very small tusks, which project almost directly downwards, and only two phalanges in all the digits except the third. The latter character has been questioned by Mr. LYDEKKER (24, p. 50), and additional characters are desirable to establish the generic distinctness of this form, which seems very closely related to *Dicynodon*.

There can be no doubt that of all these forms the type genus *Dicynodon* is the one to which the present specimen bears the closest resemblance, but at the same time there are differences which to me appear of generic importance. The spindle-shaped area inclosing the pineal fossa, the anterior part of which is formed by a triangular azygos bone, finds its nearest analogue among the Dicynodonts. This structure is not shown in any of Sir R. OWEN's figures (38), neither does Professor SEELEY (42) give a similar structure in his restoration of the Dicynodont skull. Professor HUXLEY, however

(16, p. 11), as already noticed, has described a similar arrangement of the bones of the parietal region in an Indian Dicynodont, and calls attention to specimens of *Dicynodon* [*Ptychognathus*] *Murrayi*, *D. lacerticeps*, and perhaps *Oudenodon Grayii*, as also possessing a single intercalary bone, interposed between the parietals and frontals, and bounding the parietal foramen. A similar intercalary bone is probably represented by Professor COPE (8, p. 210) as a tuberosity at the back of the frontals in *Lystrosaurus* (*Ptychognathus*).

The plan of structure pointed out by Professor HUXLEY in these Dicynodonts is no doubt in principle the same as that found in the Elgin fossil, and the Indian cranium is so similar that it may well belong to the same genus. In *Ptychognathus* (including *Dicynodon Murrayi* and *Lystrosaurus*) the form of the intercalary bone is different, and apparently distinctive, being more or less quadrate. In *Dicynodon lacerticeps* and *Oudenodon Grayii*, so far as I can see in the British Museum examples, the form of the intercalary is more like that of the Elgin skull, but it is not very clearly shown. The most important character which separates *Gordonia* from most, if not from all, Dicynodonts, namely, the possession of two large post-temporal fossæ on each side, unfortunately is not shown in the present specimen, the occiput of which is hidden; but this character is clearly seen in the allied species of *G. Juddiana* (p. 465, Plate 35, fig. 8). However, it must be noticed that Sir R. OWEN describes three such vacuities in *D. lacerticeps* (38, p. 30, Plate 23, fig. 3).

The comparative slenderness of all the bones of the skull, and the small size of the teeth in all the specimens referred to *Gordonia*, may also be taken as characteristic, and to this may be added the apparently imperfect ossification of the vertebral centra, for in none of the specimens have centra been detected with certainty, and this absence from all the examples seems to indicate something more than accidental imperfection.

There is in the British Museum a specimen of *Kisticephalus*, in which two or three vertebræ have been cut through, and these show remarkably open cancellous tissue. If our Elgin specimens had similarly ossified centra, it is possible that they would be obliterated by the coarse sandy matrix.

The peculiarities presented by this Elgin Dicynodont seem to me amply to justify its generic separation, and I propose to name it *Gordonia Traquairi*, as a mark of respect for the veteran zoologist of Elgin, the Rev. Dr. G. GORDON, and as an acknowledgement of the services rendered to science by that well-known palæontologist, Dr. R. H. TRAQUAIR, who, having recognised the affinities of this Triassic Reptile, was the first to record the occurrence of Dicynodonts in Great Britain.

2. GORDONIA HUXLEYANA, *sp. nov.* (Plates 29 and 30).

General Remarks.

The second specimen belonging to the Geological Survey is contained in several blocks of sandstone which, when placed together, exhibit impressions of a skeleton extending for about 30 inches (760 millims.) over the surfaces of the stone. These include a well preserved skull and lower jaw, with parts of scapulæ, humeri, bones of the forearm, the neural arches of some cervical vertebræ, a number of ribs, partly retaining their natural relations, and at the hinder end a portion of a pelvis with a piece of what may be a femur. The skull is in much the same condition as the first one above described, having been broken through vertically in the middle line. By clearing away some of the matrix from the left half, and by a second horizontal fracture, which exposed the temporal arcade, I have been enabled to prepare casts which reproduce the form almost as perfectly as the first specimen. The right half of the skull shows the structure of the palate in a very satisfactory manner.

Description.

Skull, upper surface (Plate 30, fig. 1).—The general form of this skull is similar to that of No. 1 specimen, but it will be seen in this view, that it is proportionately wider and more regularly oval in outline. The greatest length of the skull, making allowance for the possibly imperfect muzzle, is about 150 millims., and its greatest breadth across the temporal arcade, 100 millims. The interorbital space is about 22 millims., and the narrowest part in the parietal region 17 millims. The parieto-squamosal crest is less strongly marked than in No. 1, and its external surface (squamosal), where it slants down to the temporal fossa is nearly flat. The temporal fossa itself is broader than in No. 1 specimen. The pineal fossa is situated only a little behind a line connecting the hinder margins of the postorbital bars, while the space immediately in front of it, and between the bases of these bars, is only slightly depressed. There are indications of the spindle-shaped area, but the sutures are mostly obliterated, the median one passing backwards from the pineal fossa being alone visible. The frontal and premaxillary regions are only slightly convex from side to side. The connate premaxillæ curve downwards in front over the nasal openings, but the front is broken, and its termination obscured. However, an examination of the right half of the specimen (Plate 29, fig. 2) shows that it must have terminated somewhat as shown in the figure (Plate 30, fig. 1), there being a slight emargination of the extremity. No sutures can be traced in the front part of the skull. As it has not been possible to get a cast of the middle part of the postorbital bar, this has been modelled in the cast and restored in the figure.

Side View.—There is evidence of the premaxillæ having extended in front of the anterior nasal openings, but this is not shown on the left side (Plate 29, fig. 1). The maxilla supports a tooth very similar to that of *G. Traquairi*, but a smaller proportion of it extends beyond the alveolus. The points of the two tusks are about 20 millims. apart; a natural cast of the pulp cavity of the left one is preserved, and its base is seen immediately below and in front of the orbit. The maxilla extends backwards below the orbit, and seems to pass beyond it to join the squamosal, but these parts are somewhat broken and obscure. The jugal bone may possibly shut out the maxilla from the lower part of the orbit, somewhat as indicated by Professor SEELEY'S restoration (43), but this is uncertain; posteriorly, however, it is seen extending along the upper and inner part of the squamosal (Plate 30, fig. 1, *ju.*) forming a large part of the inner margin of the temporal bar. The squamosal, besides forming the greater part of the temporal bar, extends apparently downwards to support the quadrate and lower jaw, and upwards and forwards to form the upper boundary of the temporal fossa. In this aspect the parieto-squamosal crest is much less conspicuous than in *G. Traquairi.*

The orbit is more elongated than in the last-named species, but this may, to some extent, be due to a slight depression of the specimen.

The side wall of the brain-case is seen in the temporal fossa (Plate 29, fig. 1), but the bones are too much broken to give any definite information. Between the orbits there is a triangular bone (*o.sp.*) which may be the united orbito-sphenoids; the base of the triangle is directed backwards and the point forwards; it is bent upon itself along the middle line, so as to form a trough above and a ridge below. This bone is now towards the left side, but was doubtless a median ossification.

The back of the skull is broken and its form is uncertain.

Palate.—The whole of the upper surface of one-half of the palate is shown by the left moiety of the specimen (Plate 29, fig. 1), while the under surface is shown in the right (fig. 2). Passing back from the maxilla the anterior outer edge of the pterygoid is thickened, while further back it becomes thinner and then gives off the quadrate process. The median part in this hinder region is continued into the base of the skull. The pterygoid rises towards the middle line and forms a median ridge, which near the hinder part of the orbit rises into a thin vertical process, extending upwards very nearly to the orbito-sphenoid (Plate 29, fig. 2). On each side of this process, and somewhat more towards the front, the palate is pierced by two apertures, (*pt.f.*) as in *G. Traquairi*, but in this case the division into two by the median ridge is more clearly seen. In front of this process the pterygoid continues to rise towards the middle line, until it reaches some distance along the inner side of the orbit (Plate 29, fig. 1). This rising is really the roof of one of the posterior nares, as shown by the right half of the specimen (fig. 2), in which is also shown the ethmovomerine septum, beginning just at this point, dividing the posterior nares, and extending forwards above the arched roof of the mouth to a point as nearly as possible opposite the middle of the anterior nasal opening. This bony septum does not altogether separate the nasal cavities, its upper part evidently remained cartilaginous; near its hinder end there is an upward process which comes into near relation with the orbito-sphenoid.

The palate, as seen from below, is essentially the same as that of *G. Traquairi.* Rather more of the base of the skull is preserved in this instance, but its form is indefinite. The pterygoid gives off a quadrate process on each side, and this is definitely separated from the median part which is continuous with the base of the skull. Passing forwards the pterygoids become concave from side to side, and in the region of the pterygoid foramina the outer edges descend rapidly, then curving inwards and forwards they join the lower part of the ethmo-vomerine septum, thus circumscribing one of the posterior nasal openings. The palato-pterygoid suture is not so well seen in this as it is in *G. Traquairi;* but it is tolerably certain that the palatines surround the posterior nares, and probably form part of the pterygoid foramina.

The roof of the mouth, in front of the posterior nares, is deeply concave, with a median ridge occupying the position of a vomer, but there are no sutures visible to show what bones enter into the formation of this part of the palate.

Lower Jaw.—A large part of the left ramus of the lower jaw is preserved; but it is less perfect than that of *G. Traquairi;* on the outer side more especially the bones are broken and pushed over one another. The articular surface, however, is very well preserved; it is saddle-shaped, being convex from before backwards and concave from side to side; there is a triangular surface just in front of it on the upper aspect of the ramus, which seems to indicate that the articular element was wedged in between an outer plate (supra-angular ?) and an inner plate (splenial ?).

There are indications of a vacuity on both inner and outer surfaces; and from the lower margin a thin plate extends downwards and inwards, as in *G. Traquairi.* The imperfection of the bones prevents any useful comparison with the last-named species but the ramus appears to have rather less depth in proportion to its length.

Vertebræ.—Immediately behind the head the line of the vertebral column may be traced by portions of several vertebræ, which have the appearance of expanded transverse processes; but they are too indistinct to allow much to be said about them. No centra can be definitely made out in this or any other part of the body, although, from the position of the ribs and limbs, it is evident that the skeleton was entire when embedded in the sand.

Ribs.—Numerous ribs, or portions of them, are present, and in one block 17 or 18, more or less imperfect, may be seen lying nearly in their natural relation to each other. The longest of these, which is not complete, is the tenth in front of the ilium; it measures about 140 millims. in length, and at its middle is not more than 6 millims. wide; this, however, increases to 7 millims. at the upper end.

Ilium.—A little behind the last of the ribs there are impressions of two expanded bones, and a cast, taken from the more perfect of these, shows it to be a left ilium (Plate 30, fig. 5); the bone has been somewhat flattened, but the external surface, which is the most complete, is seen to be concave, with a thickened downward process to form the acetabulum. Only a small part of the inner surface is shown, but this is of interest, its lower part, near the acetabulum, having an articular surface, apparently for the attachment of the ischium. The greater part of the bone is in front of the acetabulum, but there is also a slight posterior extension, which is separated from the articular cavity by a notch. It is not quite certain that the upper margin is complete, but in its present condition it is undulated and nearly parallel with the lower margin. Anteriorly, it curves downwards, and, forming a rounded extremity, is continued into the lower margin, the pre-acetabular portion of which is slightly concave. The posterior extremity is indistinct, but seems to be rounded above the notch. The greatest length of this ilium is 85 to 90 millims., its least height, a little in front of the articular cup, is 35 millims., while its greatest height, including the acetabular process, is not less than 50 millims., and may have been more.

Scapula.—Parts of both scapulæ are preserved, but only one, the left, is sufficiently perfect to give an idea of its form (Plate 30, fig. 2). The lower, or articular, end is tolerably perfect, but the upper extremity is broken; when complete, it probably had more the form shown in fig. 7. Its greatest length is now 85 millims., its width, at the acromion (more correctly coracoid, Lydekker, 'Zool. Soc. Proc.,' 1893, p. 174), process, 34 millims., at the widest part above this, as now preserved, about the same, 34 millims., at the narrowest part, midway between these, 23 millims., and the neck of the articular process about 15 millims. The outer surface is convex from end to end; in the acromion region its anterior two-thirds is convex from before backwards, while the hinder third is concave. The upper part of the bone is nearly flat, but the posterior edge is reflected. On the inner aspect, the concavities and convexities are exactly reversed. The greater part of the bone has but little thickness, but the process for articulation with the coracoid and humerus is stout, and on its inner side, near the middle of the bone, there is a slight ridge. This ridge, it will be seen, is on the opposite aspect of the bone and is much smaller than that of the scapulæ figured by Mr. Lydekker (24, pp. 16 and 43), which he calls the supra-acromial process, and consequently these scapulæ have quite a different form to that of the Elgin specimen, which also differs from those figured by Sir R. Owen (38), but seems to be intermediate between that referred by him to *Dicynodon* (Plate 70) and that belonging to *Kisticephalus* (Plate 69). The acromion is more definitely marked in the Elgin form than in the latter, while there is less constriction above it. In *Dicynodon*, on the other hand (38, Plates 69 and 70), both the acromion and articular portions are more definite processes than in the present one, and there is a greater constriction above them.

The scapula of *Keirognathus* (42) is too fragmentary to allow of comparison. The portion of a scapula preserved in the specimen of *G. Traquairi* agrees, so far as can be seen, with the present one.

Clavicle.—Very near to one of the scapulæ is a spatulate bone (Plate 5, fig. 3) with one extremity produced and rod-like. This I take to be a clavicle; it corresponds in form, to some extent, with the bone of *Kisticephalus* represented by Sir R. OWEN (Plate 69), and called episternum. The broad end of this bone is thin, and the side represented is convex, while the opposite side has the appearance of having been overlapped by another bone, a ridge occupying one side and continuing into the elongated rod, as shown in the example represented by fig. 6, which occurs on specimen No. 5, and presents the opposite side of a similar bone.

Humerus.—Portions of both humeri are present, but unfortunately in a very imperfect condition; the right and more complete one is figured (Plate 30, fig. 4), but both ends are wanting. The portion preserved is the middle of the shaft with part of the deltoid crest, and the entepicondylar foramen. The crest is set at an angle with the distal extremity, and both ends were evidently expanded in the characteristic Anomodont fashion. This humerus may be compared with those figured by Mr. LYDEKKER (22, Part 3) from India, as similar parts are preserved, but nothing very satisfactory can be said about so imperfect a specimen.

Affinities.

There can be no question as to the close resemblance between the skull of this specimen and that of *Gordonia Traquairi*, and without any hesitation it is placed in the same genus. But the question of species is not so easily settled, the two skulls being so much alike and there being so few of the other parts of the skeleton available for comparison. When the skulls, or the drawings of them, are placed side by side, the differences are more apparent, and justify, as I think, their specific separation. Disregarding the difference of size, the skull of the present specimen is proportionately wider in the temporal region, although the broad outer plate of the temporal arch is narrower than in *G. Traquairi.* The fronto-nasal portion is comparatively flat, showing neither the deep depression in front of the pineal fossa nor the strongly arched nasal region. The parieto-squamosal crests also, are far less developed, and their outer surfaces are nearly flat, not rounded as in *G. Traquairi.* The entire skull is more depressed; the extreme depth from the crest to the quadrate, making allowance for imperfections, is about half the length from the hinder end of the squamosal to the point of the tusk; while in *G. Traquairi* the depth is more than three-fifths of the length measured from the same points. The lower jaw also seems to show a correspondingly greater length in proportion to depth. Although the fragment of a humerus preserved with *G. Traquairi* is too little to say much about, yet it is more ponderously developed in proportion to the size of the skull than that of the specimen now under consideration.

These points of difference seem to me to indicate more than mere individual variation, and I propose to name this form specifically after my respected master in science, who has done so much towards the elucidation of the structure and relations of the Elgin Sandstone Reptiles; it will be named, therefore, *Gordonia Huxleyana.*

3. Gordonia Duffiana, *sp. nov.* (Plates 31–33).

General Remarks.

The series of specimens from Cuttie's Hillock, belonging to the Elgin Museum, will now be described, and the first to be noticed is the greater part of a skeleton contained in several blocks of sandstone. Unfortunately most of the blocks were unnumbered when they came into my hands, and it was only by fitting the pieces together that one could tell to which specimen the different pieces belonged; this, however, was satisfactorily accomplished in all cases except with regard to the skull and trunk now to be considered; for although it is almost certain that these belong to the same specimen, yet the corresponding surfaces, by which they fitted together, could not be traced. The skull is contained in two blocks, which had been split apart when I first saw them, one half revealing the impression of part of the upper surface of a skull, about 4½ inches in length, while the other half exhibited the impression of the under side of the same parts. As it was evident that other portions lay hidden in the matrix a careful exploration with the chisel was made, the result being the opening out of both orbits, the palatal region of the left side, with part of the side wall of the brain case, and also much of the back of the skull and quadrate bone on the left side.

The impressions on the remaining three blocks represent the vertebral column, ribs, parts of the pectoral and pelvic arches, with a humerus and certain foot bones.

Description.

Skull, upper surface.—A cast taken from the upper rock-mould shows the structure of a large part of the upper surface of the skull (Plate 32, fig. 2), which is very similar to that of the two skulls above described. The supratemporal fossa is large and occupies a considerable part of this upper surface, its anterior margin being as nearly as possible the middle of the length of the skull. The parieto-squamosal crest is wider than that of *G. Huxleyi*, but does not attain to the height of that of *G. Traquairi*. The crest sweeps backwards and downwards to form the temporal bar and the pedicle for the lower jaw. The temporal bar is a thin plate, convex above and concave below, narrowing as it passes forward to join the postorbital bar, which is preserved on the left side and defines the hinder boundary of the orbit; the upper margin of the orbit is shown on both sides, and its lower limit is tolerably well defined by the remains of the suborbital bar of the right side (Plate 33, fig. 2). The inter-orbital width is 26 millims., and this is rather greater than the inter-parietal width, which is 22 millims.

A spindle-shaped area occupies the median part of the upper surface, and is similar to that mentioned in *G. Traquairi*, but larger than in that species, although the skull of the present specimen is really smaller. The pineal fossa is situated chiefly in the hinder half of this area, formed doubtless by the two parietals, the median suture passing backwards from the fossa being here well seen. An indented line on the left side near the front of the pineal fossa (but not seen on the right side) is doubtless one of the sutures which separate the anterior half of the spindle as a separate bone; and the sutures which mark its division from the frontals are also clearly indicated. From the anterior end of the spindle a ridge passes forwards to the front of the specimen, so far as the upper surface is preserved, and a median suture dividing the pair of frontals accompanies this ridge. On each side a suture is seen passing from the middle of the spindle obliquely forwards to the orbit, separating the frontal from the bone forming the postorbital bar. The similarity between the parietal region of this specimen and that of the Indian skull, described by Professor HUXLEY (16), has been already alluded to when considering the affinities of *G. Traquairi.*

Side of Skull.—The structure of the side of the skull has to be interpreted, almost entirely, from the impressions of the inner sides of the bones (Plate 33, fig. 1), but the outlines of the upper part and of the supra-temporal bar are defined by the cast of the upper surface, which has just been described, and is shown in profile (Plate 33, fig. 3), in its natural position upon the internal cast, with the missing anterior parts indicated in outline.

At the front of the specimen there is evidence of an oval opening, which has quite the appearance of being a terminal single nasal aperture, and, without the evidence afforded by the other closely allied forms, there was nothing to hinder this interpretation; but, as the premaxillary portions are wanting, it is only reasonable to suppose that, when perfect, this skull also had double anterior nares. What remains of the pre- and sub-orbital regions are best seen on the right side (Plate 33, fig. 2). A portion of the maxilla is shown just below and in front of the orbit, and there is at this point a cast probably representing the pulp-cavity of a tooth; but nothing can be seen of a similar cast on the left side. If there were two of these pulps, the teeth growing from them must have been smaller and nearer the middle line than are those of *G. Huxleyana.*

The impression seen on the right side below the orbit is probably a cast of the under surface of the maxilla; while that on the left side may represent a part of the jugal bone.

The maxillary continuation of the temporal arcade was, no doubt, very similar to that of *G. Huxleyana,* and fig. 3 has been restored on the same lines, so that the parts which are preserved may be more intelligible.

The distal articulation of the quadrate has left a saddle-shaped cavity, which is slightly out of position, and separated from the pedicle formed by the squamosal, on the back of which there is an arched space, that seems to have been for the attachment of the quadrate.

Palate.—At the time when this skull was chiselled out its affinities were entirely unknown, and, in order to ascertain whether it possessed palatal teeth, it was thought best to work down upon this region from above, so that the impression of the lower surface might be preserved. For this purpose the matrix was removed from the left temporal fossa, and the quadrate process of the pterygoid, which was soon uncovered, was traced inwards, and then the pterygoid was followed backwards and forwards. Not a trace of a tooth could be found, and the thinness of the bones, which were only a little thickened at the edges, made it highly improbable that they ever supported any dentary apparatus. The palate was displayed as far forwards as the internal nares and maxilla, and inwards beyond the middle line. In order to trace the more anterior parts of the palate, an attempt was made to display the right side from below, but without success, the bones of this side not being in place, and had evidently been broken away before the skull was imbedded in the sand; however, some additional information was obtained. The right quadrate process of the pterygoid seems to have been broken and crushed downwards as a thin vertical plate, presenting a very misleading appearance, as if it were an inner projection of the left pterygoid. If this were the correct interpretation, and the right pterygoid were absent, which seemed quite possible, the hinder part of the palate must have been much wider when perfect, with a space between the hinder ends of the pterygoids, much as in *Sphenodon.* The interpretation of this palate was indeed very uncertain until the two Survey specimens (Nos. 1 and 2) were developed; in the light of these, however, there can be little doubt that all three are constructed on the same plan. The concavity of the under surface is similar; there is the same rising in front to form the arch of the posterior nares; the hinder part, also, is evidently continuous with the base of the skull, and there is a similar process to the quadrate. Moreover, there is a corresponding perforation of the pterygoid just behind the posterior nares, but in this case, the left aperture being a little removed from the middle line, it seems clear that the two openings were more distinctly divided than in the other two specimens, and this is in accordance with the greater width of the palate which the present specimen exhibits. The ethmo-vomerine septum is shown on the under surface, but it does not appear in the section of the nasal chambers presented by the truncated muzzle.

The drawing of the palate (Plate 33, fig. 4) has been chiefly made from a cast of the left side, but also in part from measurements of the impression, and the opposite side has been restored so as to give a better idea of its width, which is absolutely greater than that of the larger skull of *G. Traquairi* (Plate 28, fig. 2).

Back of Skull.—The back of the skull in this specimen, although unsatisfactory, gives more information than either of the others, except No. 7 described below. The impression seen on the stone (Plate 32, fig. 1, and Plate 33, fig. 1) above and behind the articular condyle of the quadrate, is really the mould of the greater part of the left half of the occiput, and a cast taken from this exhibits much of its structure (Plate 32, fig. 3). The supraoccipital region can be traced descending almost vertically for perhaps 16 millims., and at this point probably the *foramen* *magnum* began, but this cannot be definitely seen. Laterally the supraoccipital region is continuous with the broad squamosal plate. From the lower part of the exoccipital region a broad bar of bone extends outward to abut upon the lower part of the quadrate (or possibly squamosal); it occupies the position of the paroccipital process of *Iguana*, and like it may be in part formed by the exoccipital and in part by the basioccipital. Professor SEELEY (43) regards this process as the homologue of the malleus. Comparing this specimen with No. 7 (Plate 35, fig. 8) it is clear that the aperture above this paroccipital process is the lower post-temporal fossa, which is separated from an upper post-temporal fossa by a process from the side of the foramen magnum, corresponding with that in *Iguana* and other Lizards, which Dr. W. K. PARKER has shown to be chiefly formed by the opisthotic. In the present specimen the upper fossa is obscure, but may still be seen. Between the two processes in *Iguana*, the *columella auris* passes to the deep-seated *foramen ovale*, and it seems tolerably certain that this was also the case in the Elgin *Gordonia*, indeed there is an angular notch at the hinder margin of the squamosal, which seems to indicate the position of the outer end of the columella.

What may be the relations of the supraoccipital, parietal, and squamosal, in *Gordonia*, there is no evidence to show; but in so far as the parts above described are concerned, the occiput of *Gordonia* seems to be constructed on the same plan essentially as that of *Iguana*.

Vertebral Column.—The block of sandstone containing the trunk, having been split open, now forms three slabs, exhibiting the counter parts of various portions of the skeleton. The most interesting slab is that shown on Plate 31, about one-third its natural size, where the vertebral column may be traced from one side to the other, and was evidently continued into the surrounding rock. The entire length of the series of vertebræ preserved being about 18 inches (460 millims.). When first examined the position of the vertebral column was indicated by the direction of the ribs, and by a double series of holes extending for a good part of its length. A closer study showed these pairs of holes to be the moulds left by the sides of the neural arches, the rod of matrix between them being the cast of the neural canal, and the neural spine passed down into the matrix; it seemed tolerably certain, therefore, that the centra of the vertebræ would be found in the opposing slab of sandstone, but this was not the case, for no traces of centra could be found. Near the front part of the specimen some of the ribs were folded across in such a way that it seemed very unlikely indeed that the vertebræ could have been displaced; and on clearing away the matrix, the pairs of holes were found, marking the positions of the neural arches; but there were no traces of centra. A little below the line of the vertebral column, and just behind the lower ribs, there is a ring-like depression, and in the opposing block there is a similar and corresponding depression; it is just possible that these may be the impressions of the ends of a deeply bi-concave vertebra; but I am by no means sure that such is the case. The form of the upper parts of the neural arches has been ascertained by removing the cast of the neural canal, and some of the surrounding matrix, from two or three of the middle thoracic vertebræ, and then taking a cast of the upper surface thus revealed. Figures of these casts are shown on Plate 32, figs. 3 and 4. The form of the neural spines is not quite certain, as the cavities were too small to allow of casts being made, but measurements were taken, and the form as given is fairly accurate. Seen from above (fig. 4) the vertebra is wide anteriorly (25 millims.) and narrow posteriorly (about 10 millims.), where it articulates with the succeeding vertebra. A side view (fig. 3) shows the anterior part depressed, while the posterior part rises considerably and arches over, as it were, to articulate with the next vertebra. A distinct ridge runs along the middle line, and posteriorly rises into a long and narrow neural spine.

Ribs.—Ribs are seen, more or less in their natural position, on both sides of the vertebral column, and on one side as many as 16 or 17 may be counted in a regular series, those towards the front being the largest. The tenth or eleventh rib from the sacrum is one of the largest and most perfect; in length it measures 180 millims., in the middle it is about 6 millims. wide, increasing to 8 millims. a little before its expansion to form the simple head, which has a diameter of 14 millims. The whole of the rib, including the head, is flattened.

Sacrum and Ilium.—At the hinder part of the specimen (Plate 31) there are three vertebræ which call for special attention, they are indicated by three pairs of holes—casts of their neural arches—from which transverse processes pass outwards for about 12 millims., and meet at an angle a broad plate, the form and position of which, leaves no doubt that it is a left ilium. The cavities left by the transverse processes and ilium are continuous, and the bones, therefore, must have been in close contact, if not firmly fixed, to each other. The ilium is partly hidden, the upper edge being under the vertebræ, but its form is shown by a cast (Plate 32, fig. 7). The greatest length of this bone from before backwards is 63 millims., the depth in front about 28 millims., increasing to 30 millims., and, with the acetabulum, 40 millims. The acetabulum, as preserved, is about 20 millims. across.

There are indications of a fourth vertebra supporting the ilium, and thus forming part of the sacrum, behind which three triangular impressions seem to be the neural spines of caudal vertebra, thrown a little out of place.

The cavity left by a long-bone is seen near the ilium, and from its position might be a femur, but it is not sufficiently perfect for identification.

Pectoral Arch.—At the anterior end of the counterpart of the block which has been figured there are some indistinct and imperfect impressions, seemingly of a scapula and coracoid, but their outlines cannot be traced. Not far from them is a very conspicuous cavity, which has been followed deep into the stone, and a cast from this (Plate 32, fig. 6) shows it to be a bone narrow in the middle, but broad and flattened at the extremities, which, however, are imperfect and set at right angles to each other. That this bone is a humerus is tolerably certain, and that the lower end in the figure is the distal extremity, wanting its articular portion, is equally certain. The proximal end is evidently imperfect, and the peculiar form shown by the cast may be, and probably is, due to this imperfection. The broad ends of this humerus conform to the Anomodont type, and whatever may be their exact form, this bone differs from the other humeri described in this paper in having its extremities set at right angles to each other, and in its more slender proportions.

Foot Bones.—Near the lower part of the specimen and midway between the extremities there are three toe bones, an ungual and two other phalanges, lying very nearly in their natural relation to each other. The total length of the three bones is 47 millims. There is no evidence to show whether these bones belonged to a fore or hind foot.

Affinities.

The necessity of including the present specimen in the same genus as the two forms already described will be obvious, but there are differences which sufficiently justify a specific separation. Of the anterior part of the muzzle, and of the teeth, one can say little, but the more median position of the teeth, as indicated by the one pulp cavity, deserves to be noticed. The upper surface of the skull is the part of which we have the most certain evidence, and when due allowance is made for possible distortion, the following points of difference between it and those of *Gordonia Traquairi* and *G. Huxleyana,* may be noticed. Although this skull is smaller than either of the other two, yet the spindle-shaped area enclosing the pineal fossa is more strongly marked than in *G. Huxleyana,* and larger than in *G. Traquairi;* its inter-orbital and inter-temporal spaces are as wide as in *G. Traquairi,* and absolutely wider than in *G. Huxleyana.* This greater width of the median parts of the skull is further exemplified by the proportionately wider palate. To these differences in the skulls must be added the slenderness of the humerus in the present specimen, and especially the peculiar manner in which its two extremities are set at right angles to each other. If the outlines of the ilia are correct, then the preacetabular extension of that of *G. Huxleyana* is another point of distinction.

With imperfect specimens to deal with, it is not always easy to give definite characters for the distinction of the species, but it seems to me that the differences just pointed out are quite sufficient for the separation of the present form, and I willingly adopt the suggestion of Dr. GORDON, to associate it with the name of Mr. PATRICK DUFF, the first discoverer of Reptile remains in these Elgin Sandstones, and call it *Gordonia Duffiana.*

4. GORDONIA TRAQUAIRI? (Plates 34, 35.)

General Remarks.

This is the second specimen from Cuttie's Hillock, belonging to the Elgin Museum. The whole of the piece of sandstone containing this skeleton has not been preserved; but the one large block, and three or four smaller pieces which have been sent to me (Plate 34), contain impressions of the greater part of the skull, with portions of the vertebral column, ribs, fore limb, and hind limb of an animal smaller than any of those yet noticed. The hinder part of the body being very imperfect, the length of the skeleton is uncertain. Much work with the chisel was necessary before casts could be taken, and, in the case of the skull, the parts being in different blocks, the joining of the casts was troublesome, especially as one side of the skull was pressed out of place.

Description.

Skull, upper surface.—Seen from above this skull is long and narrow (Plate 35, fig. 1), and resembles, in this respect, *G. Traquairi*, although only half its length, rather than either of the other species. The narrowness may be to some extent due to compression in fossilization, but the width between the orbits has not been thus affected. The left temporal bar is not quite perfect at its outer edge, but it has been completed in the figure by reference to the right side, which, although out of place, is entire. The front half of the pineal fossa is preserved, but some of the median parts of the skull behind this are wanting, however, the left parieto-squamosal crest is entire, and this shows how little is really absent. In front of the pineal fossa is a large triangular space, quite as large as that in *G. Traquairi*, but no sutures can be seen. The inter-orbital space is deeply concave, and in front of the premaxillary region curves downwards to the muzzle, which is not quite perfect, being broken away in front of the nasal apertures.

The greatest length of the skull is 93 millims., and was probably 98 millims. when complete; the greatest width across the temporal arches, as nearly as can be measured, is about 55 millims.; the least inter-orbital space is 17 millims. and the inter-temporal space was probably 14 millims. The greatest height of the skull from crest to quadrate is as nearly as possible 50 millims.

Side View (Plate 35, fig. 2).—Excepting in its smaller size, this skull so closely resembles that of *G. Traquairi* that one description would almost serve for both; but it will be seen that the parieto-squamosal crest is flat on the lateral aspect, not rounded, and it is not so high as in *G. Traquairi*, moreover the orbit is more oval in outline, being 27 millims. long and 19 millims. high, otherwise there is the same sweeping round of the crest to form a projection at the back of the skull and then to join the temporal bar and the pedicle for the lower jaw. The temporal arcade is broad, thin, and concave below; narrowing anteriorly it becomes rod-like where it joins the post-orbital bar, and with the maxilla forms the lower boundary of the orbit. No sutures can be seen to indicate the extent of each of the bones. The squamosal below the temporal arcade is a broad bone similar to that of *G. Traquairi;* curving downwards and forwards it forms a narrow neck, just above the quadrate condyle, but no division between the two is visible. The lower surface of the maxilla is concave, and its outer and lower edge is sharp, terminating anteriorly in a point, but whether this bone supported a tooth or not I am unable to say, there being no evidence of the projection of any such tooth beyond the bone, or any cast of a pulp cavity visible. The direction of the point of the maxilla is, perhaps, more downwards than in any of the forms above described. On the right side about half of the external nasal aperture is preserved, it is 11 millims. in advance of the orbit and about 10 millims. high. The extremity of the muzzle, perhaps 5 millims., is wanting.

Palate.—The outer and part of the upper surface of the palate is shown, and agrees very closely with those previously described. The median hinder part rises somewhat to join the base of the skull, but this part is obscure; the lateral process is seen extending outwards and downwards to the quadrate; the outer border is thickened before reaching the maxilla; the anterior half rises rapidly to form the roof of the posterior nares. I am unable to speak with certainty as to the presence of the aperture which in the other specimens pierces the pterygoid.

Lower Jaw.—One ramus of the lower jaw is seen extending from the quadrate to near the maxilla; but it is very imperfect, and little can be said about it except that there is no reason for thinking it differed materially from those already described.

Vertebræ and Ribs.—Vertebræ and ribs, more or less in position (Plate 34), may be traced for nearly 12 inches (300 millims.), but all are fragmentary. At a distance of about 25 millims. from the skull there is a series of four neural spines, seen from the side, which occupy a space of 40 millims.; each spine being about 10 millims. high and 8 millims. wide. Below there are the displaced neural arches, with apparently the pre- and post-zygapophyses. A long search failed to reveal any evidence of the vertebral centra, either below their neural arches, or anywhere on the specimen. The position of the hinder part of the vertebral column is indicated by fragments of ribs. Towards the anterior end of the specimen there are a few more perfect ribs which seem to be in their natural positions; they have simple rounded heads, and the most perfect one measures about 80 millims. along the outer curve, and at its broadest part is about 4 millims. wide.

Pectoral Arch. Scapula.—The hollow moulds of the bones of the left fore limb are preserved almost in their natural relations, the foot bones alone being displaced. Casts from these cavities, although representing but one side of each bone, give their characters in a very satisfactory manner (Plate 35, figs. 3 to 5).

The *scapula* (fig. 3) exhibits the outer aspect; it is a thin plate with the outer surface convex in the direction of its length, which is 59 millims.; it is widest at its upper extremity (29 millims.) becoming narrower at about the middle of its length (16 millims.); it expands a little to form the acromion process (17 millims.). Below this the bone is suddenly narrowed to 10 millims., and then more gradually, till it reaches the constriction, 8 millims. wide, above the glenoid articulation, the latter articulation again expanding to 10 millims. The anterior and posterior borders are both concave. The narrow glenoid portion is somewhat thicker than the rest of the bone. It is probable that the upper end of the scapula of *G. Huxleyana* (Plate 30, fig. 2) when perfect had much the same form as this one, which most likely was surmounted by a cartilaginous suprascapula; and it is also probable that the inner surface of the present scapula possessed a similar ridge to that seen in *G. Huxleyana.* This scapula resembles the one referred by Sir R. OWEN (38) to *Kisticephalus.*

Humerus.—The cast of this bone represents the outer and hinder surfaces, as well as the proximal and distal terminations (fig. 4). The greatest length of the bone is 56 millims.; the width of the distal extremity, 31 millims.; width from inner edge of shaft to lower angle of deltoid crest, 27 millims.; from inner tuberosity to upper angle of deltoid crest, 29 millims. The most striking peculiarity of this bone is the great width of its extremities, and the large size of its deltoid crest, the latter being directed forwards and outwards at an angle of about 75° to a line drawn across the posterior surface of the distal extremity; and with the same line the long axis of the proximal articular surface forms an angle of about 35°. The inner tuberosity is the proximal termination of the thin inner margin of the bone. The distal half of the hinder surface (fig. 4) is marked by a large triangular depression, while the proximal half is convex; its curvature, sweeping round to the side, is continued into the deltoid crest, there being no line of demarcation between them. The lower part of the crest is distinctly on the front of the bone. Between the crest and the proximal articulation there is a deep notch, but I am not sure that the angle of this notch or those of the crest should be quite so definite as they appear to be in the cast. The distal extremity, which varies from 4 to 6 millims. in thickness (fig. 4, *b*), has no definite condyles for articulation with the radius and ulna, but seems from its roughened surface to have terminated in cartilage.

Radius and Ulna.—The casts present these two bones almost in their natural relation to each other (fig. 5), and it appears to be their posterior surfaces that are preserved. The stouter of these two bones, which is regarded as the ulna, is 47 millims. long, it is narrow in the middle, 7 millims., expanding at the proximal extremity to 13 millims., and at the distal extremity to 12 millims. Its radial margin forms a thin edge, but the opposite side is much thicker. The radius is the same length as the ulna, 47 millims.; it is a stout bone, although less so than the ulna; its narrowest part, near the distal end, is 5 millims., and it enlarges gradually to the extremities, the distal being about 8 millims. and the proximal about 9 millims. wide. The inner side of this bone is marked by a groove, and seems to have a thin edge, while the other side is thickened and rod-like.

Foot Bones.—Near the distal ends of the ulna and radius are the remains of a number of small bones, evidently parts of the foot; but none of them are perfect enough to show their form.

Hind Limb.—Near the hinder extremity of the specimen (Plate 34), low down on the block of stone, is a faint impression, which may be part of the pelvis, and a fragment, about 3 inches in front of this, is probably the distal end of a femur; the surface preserved is marked by a triangular depression, which does not extend quite to the extremity. There are no indications of articular condyles, but the end has more the appearance of having been covered by cartilage.

In front of the femur are two long bones lying side by side (Plate 34); they are imperfect, a fracture of the stone having passed across both of them, but still sufficient is preserved to show their length, and that one is a little stouter than the other; they each measure 60 millims. in length, and, as this is considerably longer than the radius and ulna, they doubtless are the tibia and fibula.

Near the ends of these two bones are some scattered fragments, evidently, from their position, parts of the hind foot.

Affinities.

The structure of the skull of this specimen conforms so precisely to the type of *Gordonia* that it must be included in that genus. And there is so close a resemblance to *G. Traquairi*, except as regards size, that there is great difficulty in pointing out any satisfactory characters for its specific distinction. Unfortunately, *G. Traquairi* has no limb bones sufficiently perfect for comparison. The greatest differences between the two skulls seem to be the more elongated orbit of the present specimen, the larger size of its spindle-shaped area, the less depth of its nasal region, the less development of its parietal crest, and its much smaller size. These differences, with the exception perhaps of the first, may be due to age; and it will be well therefore, in the absence of more definitely distinctive characters, provisionally to refer the present specimen to *Gordonia Traquairi.*

5. GORDONIA HUXLEYANA (Plate 30, figs. 6–9).

General Remarks.

The third specimen from Cuttie's Hillock sent to me from the Elgin Museum is contained in three pieces of sandstone, and consists of the impressions of similar parts of a skeleton to that last described—namely, parts of the skull, vertebral column, ribs, and pectoral arch, but representing a somewhat larger animal.

Description.

The Skull is in a very dilapidated condition, the scattered fragments of it, remaining near the anterior part of the spinal column, being too indistinct to give any idea of its original form.

The Vertebræ and Ribs are in much the same condition as those of No. 4 specimen. A few neural spines may be seen, and below them crushed fragments of what are most probably neural arches. With regard to the vertebral centra, there is the same uncertainty here as in all the other specimens. Some of the fragments present are undoubtedly neural arches; others may possibly represent parts of deeply biconcave centra; but this is very uncertain. Numerous ribs are to be seen at the sides of the vertebral column, but they present no special characters; they are rather flatter than those of No. 4 specimen, and perhaps resemble more nearly those of No. 3.

Pectoral Arch. Scapula.—Parts of both scapulæ are preserved in this specimen; but the right one is the more perfect (Plate 30, fig. 7). It closely resembles that of specimen No. 4 (Plate 35, fig. 3), and similarly has the outer convex surface best preserved; part of the inner surface, however, is also present, and this shows the same thickening and ridge upon the inner side of the glenoid process that was noticed in *G. Huxleyana* (Plate 30, fig. 2A). In general form it agrees best with the scapula No. 4, but that of *G. Huxleyana* may have had a similar outline when perfect. The greatest length of this scapula is 72 millims.; its width at the upper extremity is 35 millims., and a little above the acromion process 19 millims.; below this process there is a rapid decrease. The glenoid region is incomplete, but no doubt it expanded somewhat as in the other examples.

Clavicle.—A clavicle has been described in *G. Huxleyana*, and a similar bone is lying just in front of the scapula in the present specimen; but in this instance it is the concave side of the bone which is shown (Plate 30, fig. 6). This clavicle is a thin plate, broad at one end and narrowing to a rod at the other, the rod being the continuation of a thickened edge which forms the convex margin of the bone. The greatest length is at least 52 millims.; the broad plate which occupies about half this length is 14 millims. wide.

Humerus.—Impressions of both humeri are preserved, and, as the cavities have been split open, I have been able to get casts of both surfaces, and thus the form of the entire bone is better shown in this specimen (Plate 30, figs. 8 and 9) than in any of the others. The proximal and distal ends have the characteristic Anomodont expansion; the deltoid crest is large, but has not the same proportionate extent as in specimen No. 4, neither has it the same angularity. The articular surfaces seem to have been cartilaginous, and this accounts for the slightly different form of the terminations in the two bones. The greatest length of the humerus is 71 millims., the width of the distal extremity 42 millims., and that of the proximal extremity, including the crest, 36 millims. On the front or palmar aspect (fig. 9) the inner part of the proximal half is rounded, and forms a strong support to the articular head, on the inner side of which there is a distinct tuberosity, while the outer part is concave, especially near the head, from the outer side of which the well-developed deltoid crest extends forwards and outwards. This crest is not angular, like that of specimen No. 4 (Plate 35, fig. 4); it is widest at its upper part, it then becomes gradually less as it curves downwards and inwards; crossing the front of the bone, it forms the bridge over the entepicondylar foramen, and ends near the inner side of the distal extremity. The distal half of the palmar surface is concave on the outer or radial side, and convex on the inner, just below the entepicondylar foramen. The inner and outer condyles are prominent. The back of the humerus (Plate 30, fig. 8) is strengthened by a stout buttress, which extends from the proximal articulation downwards and outwards to the outer side of the distal extremity; its upper part is continued forwards and outwards to form the deltoid crest, while on the inner side of its lower half there is a triangular concave space. Although the outlines of these humeri are well shown, their thickness is uncertain, the cavities they have left in the stone having been much compressed.

Affinities.

As the skull and vertebral column are too fragmentary to give any characters, it is only the scapula, clavicle, and humerus which are available for comparison; and, in the absence of any opposing characters, these are sufficiently like those of specimens Nos. 2 and 4 to justify their being provisionally included in the same genus, *Gordonia.*

The angular deltoid crest of No. 4 differs so much from the crests of the present humeri that they cannot fairly be included in the same species; on the other hand, the scapula of No. 2, *G. Huxleyana,* in so far as it is preserved, agrees pretty well with that of the present specimen, although it seems to be more stoutly built, and the same may be said of the clavicle and portions of humeri; but these differences may quite well be due to the impressions of the bones in the present instance having been compressed, and thus giving them a less robust appearance. The two forms agree very nearly in size, and it is deemed better provisionally to include the present one in the same species, *G. Huxleyana,* until evidence for its separation is forthcoming.

6. GORDONIA? (Plate 33, fig. 5.)

The fourth specimen from Cuttie's Hillock, belonging to the Elgin Museum, is the most imperfect of the series described in this paper. It consists of a series of impressions of the upper surfaces of from eight to ten vertebræ, to which are attached long lateral processes, nearly all in place; and, at the anterior part, some indistinct indications of bones, the interpretation of which remains uncertain. The entire length of the specimen, as preserved, is about 7 inches (180 millims.).

A cast of this specimen exhibits the upper surfaces of the vertebræ, and one or two are sufficiently distinct to show that they have a quadrate form, are rather wider than long, and a little narrower anteriorly than posteriorly. The neural spine is indicated by a tubercle placed at the hinder part between the bases of the post-zygapophyses. The most anterior vertebra which can be clearly distinguished is tilted a little out of place; it is certainly larger than the one succeeding it, and there is no doubt in my mind that the series gradually decreases in size towards the hinder end, the impressions, however, are too much worn to allow one to speak very positively. The first vertebra measures approximately 12 millims. in length from the pre- to the post-zygapophysis; in width it is 13 millims. at the front and 14 millims. at the back. The corresponding measurements of the second vertebra are—length 10·5 millims., width in front 11·5 millims., at the back 12·5 millims. The remaining vertebræ of the series are crowded together, and partly pushed one over the other.

On each side of the vertebræ are to be seen long slender processes directed backwards, and so regularly arranged as to impress one with the belief that they were processes fixed to the vertebræ, and not loosely attached ribs, which are usually found curving backwards in quite another fashion. I cannot be certain as to the point of attachment of these processes, but it seems to have been near the hinder end of each vertebra. The diminution in size of the posterior vertebræ and the presence of these transverse processes leads to the inference that they belong to the caudal region, and that somewhere in front of them the pelvic girdle would be found. As a matter of fact portions of bones have been uncovered in this region, but, unfortunately, nothing that can be definitely assigned to any part of the pelvis or limbs.

These caudal vertebræ are of Lacertilian type, and the question naturally arises, can they be referred to either of the skeletons above described, or to any of the forms known to occur in the Elgin Sandstone of other localities. They are too small for any known example of *Hyperodapedon* and much too large for *Telerpeton,* but would agree in size with some of the specimens here included in the genus *Gordonia,* and might have belonged to such a form as *G. Duffiana.* It seems quite possible that it may really be part of the specimen so named (Plate 31), but there is no information to justify this supposition, and for the present this specimen is simply referred to *Gordonia.*

7. GORDONIA JUDDIANA, *sp. nov.* (Plate 35, figs. 6 to 8.)

General Remarks.

Among the specimens sent to me from the Elgin Museum were two, to which Dr. GORDON specially called my attention because they contained pebbles similar to those found in the basal "Conglomerate bed," described by Professor JUDD (20), and presumably, therefore, were obtained from low down in the quarry near to this basal bed.

The first of these two, which I propose now to describe, consisted of a single block externally resembling in texture most of the others from this quarry; but the inner portion, immediately surrounding the fossil was, as I subsequently found, composed of much finer and softer sandstone. On one surface of this, irregular impressions and holes could be seen, some of which passed deeply into the block; and partly by cutting away the matrix and partly by splitting open the cavities, I was enabled to ascertain that these impressions represented a nearly perfect skull, slightly distorted by pressure, intermediate in size between that of No. 3 and that of No. 4. The casts taken from these cavities (Plate 35, figs. 6, 7, 8) exhibit, not only the upper and side aspects of the skull; but also the greater part of the palate and occiput; the latter including, for the first time among these Cuttie's Hillock specimens, the basi-occipital and foramen magnum.

Description.

Skull, Upper Surface.—The general structure of this skull is undoubtedly the same as in those already described, and being long and narrow when seen from above (fig. 6) resembles most nearly the skulls of No. 1 and No. 4. The distortion which the specimen has undergone prevents the true proportions being so clearly seen as in previously described specimens; the left orbit, and more especially its hinder boundary, is thrown somewhat backwards, while the right one is pushed forwards. The inter-orbital and inter-temporal regions are narrower and the pineal fossa is smaller than in No. 4 specimen, although the latter is really a much smaller skull. The frontal region is obscured, but it was evidently not depressed between the orbits. The premaxillary region is pointed anteriorly and much thickened between and above the nasal apertures by a greater deposit of bony matter than is seen in any of the other specimens from Cuttie's Hillock, and makes a slight approach to the hyperostosis seen in some of the South African forms of Dicynodonts.

Side View.—The thickness of the premaxilla (fig. 7) accompanied as it is by a similar hyperostosis of the nasal and lachrymal bones, encroaches upon the nasal aperture, which, in consequence, seems sunk in a deep pit. The maxilla bears a tooth that projects perhaps 5 millims. from its alveolus; it is directed more distinctly downward than in No. 4 specimen, and does not reach quite so far forwards as the nasal aperture. The elongation of the orbit is, to some extent, at least, due to distortion. The temporal bar most nearly resembles that of *G. Traquairi*, but differs from it and from all the specimens here noticed in having the broad hinder plate convex below instead of concave. The downward process of the squamosal is large and similar in form to those of specimens 1 and 4.

Palate.—The general structure of the palate is like those previously described; but it is narrow, even for so slender a skull, and this is not altogether due to the compression of the specimen, but seems to be a natural peculiarity, for the various parts, such as the quadrate processes, are remarkably slender. The union of the pterygoid with the base of the skull is clearly shown by this specimen, although it has been necessary to divide them in order to display other parts.

Back of Skull.—The occiput is well shown (fig. 8) and is found to possess two large post-temporal fossæ on each side, thus differing from any Dicynodont skull hitherto described. The occipital plate is, as in other Dicynodonts sunk in the hollow formed by the backwardly directed squamosal bones. No sutures can be traced and the bones can only be spoken of from the position they occupy. The occipital condyle is tripartite, the two segments formed by the exoccipitals being each much larger than the median, basioccipital segment. The lateral segments of the condyles extend upwards on each side of the foramen magnum, and being more prominent than the small median one, at first sight there appears to be a double condyle. The lower surface of the basioccipital in front of the condyle is concave. From the outer side of the condyle and lower part of the foramen magnum the bone extended outwards and downwards, forming a process abutting upon the quadrate, and is pierced by a foramen close to the condyle. In *Iguana* there is a similar process, but it does not reach the quadrate and it is chiefly formed by a process from the basioccipital. In the present specimen the larger size of the exoccipital element of the condyle and the position of the large foramen makes it highly probable that the process in this case is formed chiefly by the exoccipital. From the upper part of the foramen magnum a second process extends outwards and expands after having passed over a ridge formed apparently by the squamosal. This process abuts upon the inner side of the parieto-squamosal crest a little above the level of the temporal bar, but its true relations to the surrounding bones cannot be seen; it occupies precisely the position of the upper lateral process in *Iguana*, and like it, separates the two large post-temporal fossæ; it may still further have resembled this process in *Iguana* by being formed chiefly by opisthotic bone, and doubtless the foramen ovale was situated in the hollow just below it. A careful examination of the impressions and casts of this fossil has convinced me that both these post-temporal fossæ opened freely into the temporal vacuity.

The foramen magnum has the form of a reversed key-hole, being constricted in the middle and wider below than above. Owing to the abrasion of its margins it now appears rather too large. In its present condition it is 14 millims. high, and its greatest width is 7 millims.

Over the foramen magnum there is a depression of the bone succeeded by a prominence, above which there is a notch formed by the diverging parieto-squamosal crests.

The greatest length of this skull is 118 millims., the width across the temporal bars about 70 millims., the least inter-orbital width is 16 millims., and the least inter-temporal width about 14 millims. The pineal fossa is not clearly defined but must have been about 7 millims. long and scarcely 5 millims. wide. The height of the skull from quadrate to crest is 53 millims., but this may have been altered by the distortion of the specimen.

The lower post-temporal fossa is represented in most Dicynodont skulls, by a smaller aperture than in the present specimen, as, for example, in Sir R. OWEN'S figures (38, Plate 46, Plate 50, fig. 3, and Plate 64, figs. 6, 9). In *D. lacerticeps* the same authority (38, p. 30, Plate 23, fig. 3) describes three vacuities on each side of the occiput, of these the lower one, marked *o*, seemingly corresponds with the lower one in the present specimen, and probably leads to the auditory foramen; that marked *m* seems to occupy the position of the upper fossa, but it is very indistinct; the one marked *n* finds no counterpart in the present specimen, but may, like the small one figured by Professor COPE in his *Lystrosaurus* (8, p. 209, F.O.), represent a part of the large lower fossa of *Gordonia*, and may lead to the auditory organ, but it can scarcely be the true fenestra ovale as suggested by Professor COPE.

The occiput of No. 3 specimen seems to have the same structure as in the present skull, but the parts are more obscure and the post-temporal fossæ are proportionately a little smaller.

The Lower Jaw is indicated by a cavity to be seen below the palate, but as its anterior extremity is wanting, and the opening of the cavity would probably injure other parts of the specimen, this has not been attempted.

Affinities.

The close resemblance which this specimen bears to the *Gordonia* above described leaves no doubt as to its generic identity with them, and the structure of the occiput is so unlike that of any of the South African Dicynodonts that it affords additional grounds for the generic separation of these Elgin forms.

The distortion of the specimen prevents so close a comparison with others as could be desired, nevertheless, the positive differences seem to me sufficient to prevent its reference to any of them. In its narrowness in proportion to length this skull resembles specimens Nos. 1 and 4, but it differs from both these in the thickening of the bones above the nasal region, in the small external nasal opening, in the canine tusk being further back and more downwardly directed; also, the pineal fossa is proportionately smaller. It further differs from No. 1 in not having the same development of the parieto-squamosal crest, and this can scarcely be due to age, which the much smaller size of the present specimen might seem to indicate, for the excessive development of the bones of the nasal region in the present skull shows that it must have been an adult animal. With the skulls of specimens Nos. 2 and 3 the present one agrees in the form of its parieto-squamosal crest, but it differs from them in all those particulars which separated it from Nos. 1 and 4, and, in addition, it is proportionately narrower.

These differences seem to me amply to justify a specific separation of this form, and I purpose associating it with the name of Professor JUDD, who has done so much for Scottish geology, and was among the first to call attention to these Dicynodonts form Cuttie's Hillock. I propose, therefore, to name this specimen *Gordonia Juddiana*.

Geikia, *gen. nov.*

8. GEIKIA ELGINENSIS, *sp. nov.* (Plate 36.)

General Remarks.

The last of the series of Dicynodont remains from Cuttie's Hillock, belonging to the Elgin Museum, remains to be described. It is the impresssion of a skull in a block of sandstone which, like the specimen No. 7, includes pebbles similar to those of the basal conglomerate, and was probably obtained from low down in the quarry and near the base of these Triassic beds. The sandstone in this case is harder and coarser, making the development of the specimen correspondingly more troublesome. As the block was broken through in two directions, obliquely to the skull, the interpretation of the parts as they were exposed was rendered very uncertain, and it was not until the casts of the several parts were joined together that anything like a correct idea of the outward form was obtained. The specimen proved to be a skull of an altogether different character from that of *Gordonia*, as will be at once seen by a glance at the figures.

Description.

This skull has been a little distorted by oblique pressure, which has given a slightly different appearance to the two sides (Plate 36, fig. 1), but its general form is very obvious, and its proportions are seen to be entirely different from those of *Gordonia*. The greatest length from the tip of the muzzle to the middle of a line drawn across the hinder extremities of the squamosals is 105 millims., while the width across the temporal arches is about 125 millims.; the greatest height of the parieto-squamosal crest above a line joining the lower extremities of the quadrates would be about 80 millims. No sutures are shown, and consequently the relations of the various elements cannot be seen. The surfaces of the bones in the frontal, premaxillary and maxillary regions are rugose, but in other parts they are comparatively smooth.

Seen from above (Plate 36, fig. 1) the temporal fossæ appear almost round, the inter-temporal space is wide, 32 millims., but the inter-orbital area is remarkably so, being nearly 50 millims. at its hinder part and increasing in width towards the front, where it is 60 millims. This inter-orbital area is one of the most striking features of this extraordinary skull; each side of it is raised into a prominent ridge, which passing forwards and outwards from the post-orbital bar, overhangs the orbit, and terminates anteriorly in a thickened horn-like prominence above the nasal opening, and forms the anterior angle of the orbit. The space between these ridges is a wide semiquadrate trough 20 millims. deep. From the hinder end of each ridge the post-orbital bar passes directly outwards, it is flattened from before backwards, and curving downwards joins the temporal bar. Starting from the same point at the hinder end of the frontal ridge, the parieto-squamosal crest sweeps backwards and outwards very much as in other Dicynodonts; the two crests do not meet in the middle line but leave a space of about 14 millims.; near the front of this space the pineal fossa might be expected to be seen, but unfortunately an oblique fracture crosses this part and renders it obscure.

The premaxillary region forms a small beak-like prominence at the front of the specimen (fig. 1) which is set at an angle of about 55° to the top of the skull, as shown in a side view (fig. 2). It is flattened anteriorly (fig. 3) where it is marked by three ridges, one median and one at each side, the latter separating the front from the lateral aspects of the muzzle.

Side View.—Seen from the side (fig. 2) the pedicle for the lower jaw is very long, but on the whole is very similar to that of *Gordonia*, excepting that throughout its length it is turned more directly forwards. . Probably this pedicle is formed as in other Dicynodonts chiefly by the squamosal, which also constitutes a large part of the temporal bar as it passes forwards to the orbit. The sub-orbital bar is directed inwards and a little forwards, its lower margin being continuous with the lower edge of the maxilla, which is directed downwards and forwards to end in a point evidently corresponding with that in *Gordonia* which carries the tooth; but there is no tooth to be seen here, and the thinness of the maxilla at this part makes it unlikely that there was any tooth, but points rather to its having had a horny covering. The orbit looks outwards and forwards, it appears almost triangular when seen from the side (fig. 2); its upper margin is nearly straight and meets the post-orbital bar almost at a right angle. The sub-orbital bar, in this view, seems to form an almost straight margin extending from the lower end of the post-orbital bar to the horn-like anterior end of the frontal ridge. However, when seen more from the front (fig. 3), the lower boundary of the orbit is found to be curved, and to be continued upwards by a sharp edge, probably formed by the maxilla, lachrymal, and prefrontal bones, but no sutures mark the limits of these elements. In front of and below the orbit there is a somewhat quadrate area in which the surfaces of the bones are marked by rugosities; these are best seen on the right side (figs. 2, 3). One angle of this area is directed downwards and forwards, it forms the anterior extremity of the muzzle, and is doubtless the premaxilla. A second angle directed downwards is the tooth-like point of the maxilla. The thickened angle directed upwards, is the horn-like prominence possibly formed by the prefrontal. The hinder angle is that at which the sub-orbital bar joins the maxilla The margin between the points of the maxilla and premaxilla is deeply indented; it forms a sharp cutting edge and was in all probability covered with a horny armature; this edge, with a portion of the maxilla behind its point, formed the upper oral margin. The edge uniting the premaxilla and the prefrontal (?) is likewise indented, and a little behind the angle thus formed there is a deep fossa in relation to the anterior narial opening, but the true aperture seems to be restricted to a small part near the anterior margin, and cannot be seen very clearly on account of the matrix.

Passing backwards and inwards from the maxilla is the pterygoid, which has much the same form as in *Gordonia*, but is relatively shorter and deeper. This will be alluded to again when describing the palate.

Front view.—Seen from the front (Plate 36, fig. 3), the skull shows some of its peculiarities in a striking manner—the large inter-orbital trough, with its ridges terminating in front and above the orbits, as horn-like prominences, which overhang the widely-separated external nasal openings. The flattened and triple-ridged premaxillary area is also best seen in this aspect. The orbits, as in the side view, appear to be nearly triangular, while below and in front of them the maxillæ extend downwards to form the pair of prominent but toothless projections. The right squamosal and quadrate are seen in this view, those of the left side are partly wanting.

Palate.—The palate has essentially the same structure as it has in *Gordonia* and other Dicynodonts. The hinder part, where it joined the base of the skull, is broken away, but the front part, although somewhat distorted, gives full information as to its general structure.

The roof of the front part of the mouth is deeply vaulted, and forms an arch extending backwards some little way beyond the tooth-like maxillary processes. This arch is formed by inwardly-directed plates from the maxillary and premaxillary regions, and it is highly probable that it was terminated posteriorly by the palatines, which may here, as in *Gordonia*, have formed the greater part of the boundary of the posterior nares. The pterygoids may, perhaps, have taken part in the completion of the hinder boundary of this vault, while the thickened ridge in the middle line of its hinder two-thirds occupies the position of a vomer. Above this ridge there was an ethmovomerine septum dividing the nasal chambers. The form of the posterior narial opening is hidden, but it is pretty clear that its front margin was situated about 10 millims. behind the maxillary tooth-like process, and was divided by the ethmovomerine septum. The pterygoids are deeply arched where they rise to cover over the posterior nares, and at the hinder part of this arch they are pierced by two narrow openings which are separated above by a median septum, and occupy a similar position to the pterygoid foramina of *Gordonia*. The pterygoid is preserved for 45 millims. behind the maxilla, but beyond this the palate and base of the skull is broken away. However, the quadrate processes of the pterygoids were traced on both sides to the neighbourhood of the quadrates.

Back of Skull.—The back of the skull is very wide and flat (Plate 36, fig. 4), the squamosal crests above, and the quadrate pedicles at the sides projecting but little beyond the plane of the occiput. The foramen magnum is large and oval, but its lower part is imperfect, resulting from the breaking away of the articular condyle, and it may be that when perfect, it was not quite so large as it now appears to be. The basioccipital is much broken, but on the right side there is a prominence indicating a downwardly-directed process in the position of the hypapophysis present on each side in most of the South African Dicynodonts. Each exoccipital is pierced by a large foramen just in front of its condylar portion, it extends outwards and downwards as a large process and abuts upon the quadrate region of the pedicle. There is no trace of a suture to separate this process from the exoccipital. Immediately above the process is a large post-temporal fossa, evidently corresponding with the lower one seen in *Gordonia Juddiana* (Plate 35, fig. 8), and to that present in some of the South African specimens figured by Sir R. OWEN (38, Plate 23, figs. 3 and 10, and Plates 46 and 50), and Mr. LYDEKKER (24, pp. 28, 34, 41); it does not correspond with those marked *m* and *n* in Sir R. OWEN's figure (38, Plate 23, fig. 3), but may in part with that marked F.O. by Professor COPE (8, p. 209).

The upper half of the occiput is formed by a plate of bone confluent with the squamosal ridges on each side and presenting no sutures to indicate what part each element takes in its formation.

Lower Jaw.—The impression of the lower jaw is well preserved, showing parts of both rami, and most of its structure very distinctly (Plate 36, fig. 5); the symphysis and articular end of one ramus being entire. Its greatest length is 88 millims.; the characteristic fossa on the outer surface is 33 millims. long. There is a broad, thin plate of bone passing downwards and inwards from the lower margin, similar to that which has been described in *Gordonia.* This plate seems to be connected with the lower and hinder part of the dentary element, which appears to extend far back, this, however, is by no means certain. The two rami are co-ossified at the symphysis, which is wide, especially below, and oblique as seen from the side. The whole of the symphysial region is rugose, and the upper front part of each ramus is produced into a warty, tooth-like prominence; while the upper margin of each ramus, for some distance behind the prominences, is flattened, leaving however, a groove between the two sides, which may have been connected by bone for 20 millims. from the front. The appearance of the whole symphysial region favours the supposition that it was covered by a horny beak, produced in front into a pair of large horny teeth. The least depth of the jaw, just behind the symphysis, is 20 millims.; from this the upper margin rises to above the middle of the lateral fossa, and then rapidly sinks to its former level and curves backwards to the saddle-shaped articular surface. The angle of the right ramus curves downwards and forwards, that of the left side is not shown.

The vertical extent of this lower jaw is proportionately less than in *Gordonia,* although the height of the skull might lead one to expect that it would be greater.

Affinities.

Although the external form of the skull is unlike any Dicynodont hitherto described, yet the formation of the palate, of the occiput, of the maxilla, and of the lower jaw, are sufficient to establish its close alliance to the forms which are included in this group. The great width of this skull in proportion to its length, and the angle formed by the meeting of the premaxillary and frontal regions, point to *Ptychognathus* as its nearest ally. The occiput of *P. declivus* of Sir R. OWEN (38 Plate 46, fig. 1), is very like that of the present specimen (Plate 36, fig. 4), and the great width between the orbits is likewise very similar in the two forms. The frontal region is somewhat hollowed in some species of *Ptychognathus*, although not to the same extent that it is in this Elgin fossil.

On the other hand, while in *Ptychognathus*, the premaxilla and maxilla are much produced, and the latter bone bears a large tusk, in the present specimen there are no tusks, and these bones are comparatively short. The great size of these bones in the former case is obviously correlated with the largely developed tusk, but this does not altogether account for the differences observable. The similarity between the skulls of some species of *Dicynodon* and *Oudenodon*, excepting the want of tusks in the latter, led Sir R. OWEN and others to suggest the possibility of this being merely a sexual character; and the present toothless form seems to hold a somewhat similar relation to *Ptychognathus*. However, the evidence has not been found sufficient to justify the union of the two genera last named, and still less are we in a position to unite this Elgin toothless skull with the large-tusked and long-snouted *Ptychognathus*, more especially as the latter genus has not been found in the Elgin rocks. There will be no question, therefore, as to the desirability of establishing a new genus for the reception of this fossil, and I propose to associate it with the name of Sir ARCHIBALD GEIKIE, the Director-General of the Geological Survey, while specifically it will be convenient to suggest the neighbourhood where the specimen was found; it will therefore be known as *Geikia Elginensis*.

GENERAL REMARKS ON ELGIN DICYNODONTS.

The very close resemblance in point of structure between the skulls of all the specimens above referred to *Gordonia* is a sufficiently clear indication of their generic identity; while the characters which they possess in common show unmistakably that they belong to the Dicynodontia, and are most nearly related to *Dicynodon* and *Oudenodon*. The small size of the teeth seems to indicate an intermediate position between these two genera, but as the absence of teeth is the chief character by which *Oudenodon* is separated from *Dicynodon*, the Elgin specimens would seem to be most nearly related to the latter. Nevertheless these Elgin forms present, as I think, distinctive characters which justify their being placed in a separate genus, for which I have proposed the name *Gordonia*.

Gordonia is characterized by the presence of two post-temporal fossæ on each side of the occiput, by the comparative slenderness of all the bones of the skull, by the small size of the maxillary tusk, and probably by the elongated spindle-shaped parietal area enclosing the pineal fossa.

The scapula of *Gordonia* is very similar to the one referred by Sir R. OWEN (38, Plate 69, fig. 9) to *Kisticephalus*—that is to say, it is a flattened bone with a constricted neck above the glenoid cavity, and a distinct acromion process; the skull of the latter genus, however, is quite unlike that of *Gordonia*, more especially in the greater width of its parietal region.

The humerus of *Gordonia* has the characteristic wide extremities and narrow median portion, with a large deltoid crest and entepicondylar foramen.

The ilium is a broad flattened plate which thickens in the region of the acetabular cavity, and has the greater part of its mass in front of that cavity. Its extension behind the acetabulum differs somewhat in the two forms in which it is preserved, being greater in *Gordonia Huxleyana* than in *G. Duffiana*, unless in the latter it has suffered mutilation. The sacrum, shown only in one specimen, included not less than three or perhaps four vertebræ.

We have yet to learn the character of the vertebral centra, as none of the specimens give any definite evidence on this point, and the seeming absence of the centra, although the neural arches are present, is, to say the least, remarkable.

The fragment of a skull described and figured by Professor HUXLEY (16) from the Panchet stage of the Gondwana beds of Central India as *Dicynodon orientalis*, very closely resembles *Gordonia*, more especially *G. Duffiana*, and it seems far from unlikely that they may prove to be generically identical. Mr. LYDEKKER (23 and 25) has referred this Indian specimen, with others from the same locality, to the genus *Ptychognathus*, but in so far as this particular fragment of a skull is concerned I am unable to accept this allocation.

Professors COPE (8) and SEELEY (43) have discussed very fully the structure of the Dicynodont skull, and the Elgin specimens are not in a condition to contribute much to a knowledge of its more intimate structure; still a few points may be noticed upon which they seem to throw some additional light. The structure of the frontal and parietal regions of the skull in *Ptychognathus* (*Lystrosaurus*), as described by Professor COPE, and the form of these parts in *Dicynodon*, as restored by Professor SEELEY, are quite unlike the arrangement found in *Gordonia*, while the fragment of a skull from India, above alluded to, agrees very well with the Elgin genus. Although I am disposed to think some modification of Professor SEELEY'S restoration of *Dicynodon* will be found to be necessary, yet it seems to me probable that the different genera of Dicynodontia will be found each to present a peculiar modification of the bones of the fronto-parietal region. These Elgin specimens give no information which would support the idea that the bone, extending between the exoccipital and quadrate regions, is the homologue of the malleus, but rather point to this bone being merely an extension of the exoccipital, and possibly of the basioccipital, such as is seen in the skull of the *Iguana*, and the presence of a second post-temporal fossa, as shown in *Gordonia Juddiana* (Plate 35, fig. 8) corresponds so well with the structure of this region in *Iguana* and other Lacertilia that I am constrained to believe they are constructed on the same plan. And, further, that in most, if not in all, Dicynodonts hitherto described, the upper post-temporal fossa is closed in by bone, while the lower one, being that which leads to the foramen ovale, is always found open.

The arrangement of the bones forming the posterior nares in *Gordonia*, and probably in all other Dicynodonts, is exceedingly like that found in the Turtle, the palatine bones forming tubular passages which open upwards and forwards into the nasal chambers. The pterygoid foramen, present apparently in all *Dicynodonts*, just behind the posterior nares is not found in the Turtle.

All the lower jaws of *Gordonia* which have been found are characterized by the broad thin plate projecting downwards from the lower margin; this does not appear to have been noticed hitherto in Dicynodonts, which is the more remarkable, as it occurs also in *Geikia*, the ally of *Ptychognathus;* it seems likely, therefore, to be a characteristic of Dicynodonts generally.

Before proceeding with the description of a specimen belonging to a very different group of Reptiles, it may be well to give briefly the specific characters of the Cuttie's Hillock Dicynodonts.

Gordonia Traquairi.—Specimen No. 1, will be the type species of the genus; it is characterized by its narrowness in proportion to its length, by its great height from quadrate to crest, which is three-fifths of the length from the back of the squamosal to the point of the tusk. The parieto-squamosal crest is strongly developed, the spindle-shaped area is small, and the inter-orbital space forms a deep concavity especially towards its hinder part.

The small specimen, No. 4, is provisionally referred to *G. Traquairi*, and if this association prove correct, the humerus of this species will be distinguished by its angular deltoid crest.

Gordonia Huxleyana.—Specimen No. 2, for which I propose this name, is distinguished by the greater proportionate width of the skull, not only across the temporal arcades, but also between the orbits. The skull is likewise more depressed, its height from quadrate to crest being about half the length from the back of the squamosal to the point of the tusk. The upper surface is flatter than in *G. Traquairi* and does not exhibit the same inter-orbital concavity.

To *G. Huxleyana*, specimen No. 5 is provisionally referred; the humerus of this specimen having a rounded crest, is quite unlike that of the smaller form referred to *G. Traquairi.*

Gordonia Duffiana.—The type of this species is specimen No. 3. The skull is proportionally wider at all parts than that of *G. Huxleyana*, and consequently differs still more in this particular from *G. Traquairi;* it also differs from the latter species in the large size of the spindle-shaped area and the flatness of the upper surface.

The two extremities of the humerus being at right angles to each other, is an important distinction between this species and *G. Huxleyana*.

Gordonia Juddiana.—The specimen for which I have suggested this name is a skull which agrees with that of *G. Traquairi* in being proportionally narrow, but it differs in having only a slight parietal crest; the bones of the nasal region are so thickened that they encroach upon the small nasal aperture; the tusk is placed a little further back and points more directly downwards. The pineal fossa is smaller than in any of the other specimens. This skull seems to be as much depressed as in *G. Huxleyana*, but this may be owing to distortion.

Geikia is established for the reception of a skull presenting most of the characters which distinguish *Ptychognathus* from *Dicynodon;* the inter-orbital and inter-temporal spaces are very wide, the premaxillary region bears three ridges on its upper surface, which is set at a considerable angle to the frontal, or inter-orbital region, and the wide, flattened occiput shows only the lower post-temporal fossæ. On the other hand *Geikia* differs from *Ptychognathus* in having a comparatively small development of the premaxillæ and maxillæ, so that the prenasal portion is as small as in *Dicynodon*, but there are no teeth.

Until other species of this genus are discovered, the above characters will suffice for the distinction of this genus and species.

B. PAREIASAURIA.

Elginia, *gen. nov.*

9. ELGINIA MIRABILIS, *sp. nov.* (Plates 37–40).

General Remarks.

The Reptilian skull now to be described is one of the most remarkable fossils which have come to light for many years, and reminds one more of *bizarre* Reptiles discovered in North America than of anything which has been found on this side of the Atlantic. The specimen, in common with the others described in this paper, was obtained from the Elgin Sandstone of Cuttie's Hillock Quarry, and, thanks to the foresight and energy of Mr. LINN and Mr. B. N. PEACH, of the Geological Survey, is now the property of the Survey. Unfortunately, only the skull of this creature has been recovered; it is about 6 inches in length, and, like all the remains found in this quarry, is in the condition of a hollow mould, all the bone having disappeared.

The most striking peculiarity of this skull is the extraordinary development of bony horns or spines with which the surface is ornamented. There are sixteen of these horns on each side, varying in length from one-fourth of an inch to nearly three inches, besides three small bosses on each side of the parietal region; also in the middle of the forehead there is a rounded spine, and near the bases of the two nasal horns a small median protuberance, making in all forty of these bony outgrowths, which, although comparatively smooth, exhibit longitudinal grooves and striations indicative of their having been invested with horn. The surface of the bones between the horns is deeply pitted as in the skull of a Crocodile.

The block of stone containing this specimen has been split open in such a way as to peel off, as it were, the greater part of the outer surface of the upper and side walls, leaving, like a kernel, a nearly perfect cast of the inner surface of the bones, which reproduces the general form of the skull; but it is, of course, the pieces that have been peeled off which contain the impressions of the true outer surface, and these, with one or two exceptions, have been preserved. Parts of the right parietal region, and of the left cheek, are wanting; but fortunately, with one exception, what is wanting on one side is preserved on the other.

The first step in working out this specimen consisted in fitting together the fragments which made up the outer surface, and some of the parts, still attached to the main block, had to be cut away and cemented in their proper places on the outer shell. The preparation of casts from these impressions proved to be a more tedious process than with previous specimens, on account of the many separate pieces which had to be made before the whole could be fitted together. The outcome of this first part of the work was the reproduction of the external form of the skull, as shown in Plates 37 and 38.

The front part of the internal cast, or kernel, had been broken through in such a way as to expose the impression of much of the palate, but in order to trace the hinder part of this region, and the base of the skull, it was necessary to cut away, piece by piece, the left cheek with the underlying parts, and although these pieces did not always come away so satisfactorily as could be wished, they have now been cemented together and can be replaced, very little having been lost in the process. The time bestowed upon the development of the deeper parts of this skull has been fully repaid, as the casts made from them reveal the structure of the palate, the base of the skull, and the occiput, together with a large part of the brain-case. A knowledge of these parts, and of the dentition, which was afterwards exposed, was very necessary for the elucidation of the affinities of this new Reptile.

Description.

The Skull.—The right side of the skull retains very nearly its natural form, while the left side has been distorted by the pressing forwards and outwards of the large horn, with the cheek and sub-orbital region; the general contour of the head, however, is but little interfered with. The only vacuities seen on the outer surface are the orbits, the pair of nasal apertures, and the pineal fossa. The bony continuation from the maxilla to the inferior quadrate region shows that the lower temporal arcade is complete, but both the lower and upper temporal fossæ are as entirely covered in by bone as in the Green Turtle. The outer surface of all the bones, except the premaxillæ, are deeply sculptured with rounded pits, similar to those of the Crocodile, which seem for the most part to radiate irregularly from the spines and bosses. The spines, as already noticed, are longitudinally striated, and this comparatively smooth surface ends abruptly at the lower part and forms a definite edge where it joins the deeply-pitted general surface of the bones. In both upper and side views the skull is, roughly speaking, triangular; in the former view (Plate 38) the posterior margin forms the base, the angles of which are produced into the largest pair of horns, while in the latter view (Plate 37) the apex of the triangle is truncated by the deep and almost vertical muzzle.

The sutures are difficult to trace, but on the cheek and nasal regions they are indicated by deeply serrated lines, corresponding with the meeting of the radiating pittings; in other places they are indistinct. A careful examination of the inner as well as the outer surfaces, however, has led me to indicate by lines what I believe to be the general direction of many of the sutures.

As the skull of the South African *Pareiasaurus* seemed to resemble this fossil more nearly than any other form, I endeavoured to trace a similar arrangement of the bones to that described by Professor SEELEY (41, 44), but in this I have been only partially successful, although on the whole it is tolerably certain that the two skulls are constructed upon the same plan.

A front view of this skull shows the pair of large nasal apertures looking almost directly forwards, and completely separated by the upward processes of the two premaxillæ, which are seen to be separated throughout their vertical extent, a distance, from the dental margin to the bases of the nasal horns, of about 40 millims. The external surface of each premaxilla is comparatively smooth, and as this smoothness ceases suddenly on each side near the hinder part of the nasal opening, this point probably marks the junction with the maxilla, but no suture can be seen. The nasal apertures are nearly round, and each is about 22 millims. in diameter, the upper and inner part alone being angular, and here they are surmounted by a pair of coarsely striated horns probably outgrowths of the nasal bones. Another pair of horns is seen, one on the outer side of each nasal opening, and these seem to be formed by the maxillæ.

An examination of the natural cast of the nasal chambers shows that, at about 5 millims. within the outer margin of the external aperture, a thin plate of bone extends inwards for a little distance from the circumference, thus constricting the cavity and partly separating off a shallow anterior chamber.

The lower margin of each premaxilla supported four or five teeth, but these will be alluded to when the entire dentition is described.

When the *skull* is *viewed from above* (Plate 38) the two nasal horns are seen to be at the most anterior part of an area, which is separated from the frontal region by a jagged suture arising from the middle of each nasal orifice. This area must certainly enclose the two nasal bones, although no suture is traceable between them; but on the median line there is an oval raised spot, with a concave surface, which may be the remains of a small median spine. The next landmark on the upper surface is the pineal fossa, part of which is preserved, and this is situated exactly in the middle of the skull and opposite the hinder edges of the orbits. When perfect, this fossa must have been about 13 millims. long and 9 millims. wide, and between it and the fronto-nasal suture is a distance of about 50 millims. while at about 30 millims. in advance of it is a pair of horns, doubtless marking the centres of the frontal bones, but no median suture is visible; and with the exception of the fronto-nasal suture there is nothing to mark them off from the surrounding bones. Above each orbit there are three spines, the hindermost of which is the largest and is probably formed by the postfrontal, while the anterior may be the prefrontal; the middle one of the three possibly being a separate ossification. The large extent of surface behind the pineal fossa makes it probable that this fossa was placed near the front of the parietals; but to what extent these bones entered into the roof of the skull cannot be seen, and, indeed, the want of definite sutures makes the interpretation of this region difficult. The pineal fossa communicated directly with the brain cavity by a large opening; and behind this the outer bones of the skull do not form the roof of the brain case, but a large temporal fossa, open at the back of the skull, intervenes on each side, separating the true cranial roof from these outer plates. A vertical and longitudinal plate connects the inner cranial roof with the outer bony covering and, rising as it does above the foramen magnum (Plate 40), occupies the position of the supraoccipital. This bone is in relation above with the bone supporting the median horn of the forehead, which might, therefore, be part of the supraoccipital. But behind this bone, and seemingly separated from it by a suture, is a pair of bones, forming the back part of the upper surface of the skull, each of which bears a well-developed horn. These two bones are likewise in relation with the vertical median plate and, it seems to me, are much more likely to be the supraoccipital elements, while the more anterior one with the median horn is in all probability an interparietal or intercalary bone. If the median plate is the supraoccipital, what are the two hindermost ones? They can scarcely be epiotics, for two reasons; in the first place, epiotics do not meet in the middle line, and secondly, they should be in relation to the brain case and auditory region, while the two bones in question are separated from the brain case by the post-temporal fossæ, the only connection being the vertical supraoccipital plate. Externally these two bones are separated by sutures (shown on the left side) from those forming the outermost angles of the hinder border which bear the large pair of horns, and it is these which hold the position of epiotics, each being inferiorly in relation with the buttress extending from the exoccipital, which is in all probability formed, to some extent, at least, by the opisthotics. It seems to me to be most in accordance with the known relations of these bony elements, to regard the outermost pair with the large horns as the epiotics, the inner pair with the smaller horns as the supraoccipitals, and the median rounded plate with the single horn as an intercalary bone.

The internal cast in the parietal region shows, on each side of the pineal fossa, a line passing outwards and backwards, which again curving inwards circumscribes an oval area, directed towards the large horn. The position of this line is indicated on the figure of the exterior of the skull (Plate 38, *pa.*). These two areas are separated by the vertical supraoccipital plate, and the intercalary bone on the outer surface must have overlapped the inner edges of the bones indicated by these two areas, which almost certainly indicate the position and extent of the parietals. It is not certain whether the pineal fossa was entirely surrounded by the parietals.

In a side view (Plate 37) the anterior end of the skull is deep and truncated. The nasal apertures are close to the extremity, and being directed nearly forwards would be very little seen in a side view; the distortion of the skull, however, although slight, has pushed the right one a little outwards, and consequently rather more of it is seen in the figure than would naturally have been the case. The nasal bone and horn are seen above this aperture, while in front and below it is the premaxilla; immediately behind it is a spine, doubtless supported by the maxilla, which probably extended only a little way in front of the spine, but certainly reached as far backwards as the middle of the orbit, there being evidence of teeth at this point. The maxilla appears to be united above with the nasal and prefrontal bones, and posteriorly to form the front and lower boundaries of the orbit, but it is possible that a lachrymal bone may be wedged in between it and the prefrontal. The internal cast shows a very distinct canal running from the orbit to the nasal chamber, which there is little doubt is a lachrymal canal, and as it is placed rather deep in the orbit, it is quite possible that the lachrymal bone was overlapped externally by the maxilla. Professor SEELEY found no lachrymal bone in *Pareiasaurus.* The suborbital bar is broken near the union of the maxilla and jugal bones. The outline of the orbit is quadrate with rounded corners, and narrower in front than at the back; its upper margin is nearly straight and formed by the bases of the three spines by which it is overhung. The length of the orbit is 35 millims., the height is, anteriorly about 25 millims., and posteriorly about 35 millims.

The cheek behind the orbit is nearly square, and two deeply serrated sutures may be traced across it, one nearly vertical and the other nearly horizontal; besides these there is another at the base of the large horn which was probably continued along the upper margin of the cheek and separated it from the parietal region, but this latter part, as we have already seen, is wanting. On the internal cast there is a deep groove corresponding with the vertical cheek suture, but double at its upper part, which shows that the two hindermost cheek bones turned inwards, and formed the outer boundary of the lower post-temporal fossa (Plate 40, *st.* and *qu.*). The internal cast also shows some slight irregular lines corresponding with the horizontal cheek suture. The cheek is thus divided into four areas; the upper and anterior one (*pt.o.*) forms half the hinder border of the orbit, and may be a part of the bone supporting the spine at the corner of the orbit, which I have called the postfrontal; but it seems much more likely to be a separate ossification, and if so, occupies the position of a post-orbital. The lower anterior area also forms part of the orbit, and is doubtless the jugal bone (*ju.*); it bears a large outwardly directed spine close to the lower corner of the orbit. The lower and hinder cheek area supports two large and two small spines, its position is that of the quadrato-jugal and quadrate; but how much of the latter bone is seen on the outer surface is uncertain. The articulation for the lower jaw, and therefore the quadrate, is close to and within the two smaller spines, which may be parts of that bone, but no sutures can be seen; or it may be that the quadrato-jugal entirely overlaps its outer surface. It is quite possible that the lower bone seen on the inner surface may be the quadrate, and that it extends backwards to form the posterior horn (Plate 40, *qu.* ?). The upper and hinder cheek area carries a large backwardly directed spine, and is separated by suture from the bone bearing the large horn, which I have referred to as the epiotic. This cheek area must be either the squamosal or the supra-temporal bone; it certainly occupies a similar position to the squamosal of the Turtle, and I am unable to point to any definite area as the squamosal, because the region immediately above this is lost on one side and obscured on the other; but it seems to me much more probable that this skull is formed on the plan of *Pareiasaurus* and that this upper cheek bone is a supra-temporal, while the squamosal will have to be sought in the region marked *sq.* in the figure; that is to say, it will probably be found as a small ossification wedged in between the supraoccipital, parietal, supra-temporal and epiotic, and possibly the small horn at the base of the large epiotic horn will prove to be a part of this squamosal. The markings on the internal cast lend some support to the latter interpretation.

Allusion has already been made to the double groove on the internal cast, corresponding to the upper part of the vertical cheek-suture. This double groove encloses an oval area, situated at the front of the bone I have called supra-temporal (Plate 37, *st.*), and would partly take in the spine seen at the upper part of this bone. These grooves, originally occupied by bone, I have traced inwards on the left side of the skull, and find that they are continuous with the buttress (opisthotic), passing outwards from the exoccipital region to the region of the squamosal; this bone, therefore, occupies the position of the *prootic*, and it is tolerably clear that the auditory organ must have been in this region. It is not certain that this bone reached the exterior, but it seems likely that it formed the spine seen just above and behind it on the outer surface.

The *Palate* of this specimen has been thrown over to one side by the distortion which the skull has undergone, and the median parts seem to have suffered by lateral pressure; but with the exception that little can be seen of the sutures, its structure is well shown (Plate 39), and appears to me to be formed on the Lacertilian plan. This palate is short and wide in proportion to the length of the skull, and its greatest peculiarity is the relation of its hinder parts to the elongated base of the skull. The front is rounded and margined by the deep edges of the premaxillæ and maxillæ, which are continued posteriorly by the jugals and quadrato-jugals. Near the front there are two large apertures, the internal nares as I think, the more perfect one measuring 30 millims. in length by 9 millims. in width at the rounded hinder part, while anteriorly it narrows almost to a point, and the two are separated by a bony division, from 12 millims. to 15 millims. wide. These apertures open directly upwards into the nasal cavities, and they are not mere vacuities which might be due to non-ossification of membrane or cartilage, but are definitely margined openings, the inner edge of each being on a different plane from that of the outer margin and tending anteriorly to overlap it, in a manner similar to that seen in Lizards. The hinder part of the palate has been uncovered on the left side, and is found to give off a long and stout process outwards and backwards to the quadrate region. The inner end of this process is seen to arise from the side of a median aperture, behind which is the extremely elongated base of the skull. This median aperture of the palate occupies precisely the position of the interpterygoid vacuity in *Iguana* and *Sphenodon*, and corresponds with that seen behind the posterior nares of Dicynodonts; it cannot be homologous with the posterior nares of Dicynodonts or of Turtles, for in these the posterior nares are surrounded by the palatines, whereas this opening seems to be chiefly formed by the pterygoids. There is a great resemblance between the position of this opening and the posterior nares of Mammals, and Professor SEELEY regards them as such (44, p. 316), but with this I cannot agree, for reasons given below (p. 488). The quadrate process of the pterygoid bounds, posteriorly, a large triangular space, which has the quadrato-jugal arch on its outer side and terminates anteriorly close to the hindermost teeth of the maxilla. A similar vacuity is present in *Sphenodon*, and also in *Iguana;* but in the latter, there being no ossified quadrato-jugal arch in the dry skull, there is no outer boundary. And further, in the present specimen, there is a process which projects into this space from its inner side, and a similar projection is seen in both *Sphenodon* and *Iguana*, and as in both these it marks the junction of the transverse and pterygoid bones, it seems highly probable that the same is the case here also, but no suture can be traced.

That the elongated anterior palatal apertures are the posterior nares, opening directly upwards into the nasal chambers, as in Lizards, there seems to me no reasonable doubt. It is also tolerably certain that some part of the horizontal plate of the palate is formed by inwardly directed laminæ of the maxillæ and premaxillæ; very little of the latter, however, is to be seen. On the left side, there is a line which seems to be the junction between the maxilla and the palatine, and if this be so, then both these elements take part in the formation of the outer wall of the nasal opening. The space between these apertures is probably occupied by the vomers, and if the oblique lines seen on the floor of the nasal chambers, and also more faintly on the palate, are sutures, then the palatine bones are almost excluded from the inner walls of the posterior nares. No sutures can be seen, which would allow one to separate the palatines, pterygoids, and transverse bones, and it is uncertain whether the palatines or pterygoids occupy the middle part between the hinder ends of the vomers. There can be little doubt that the processes to the quadrate bones are formed by the pterygoids, and that the anterior boundary of the pterygoid foramen is formed by the same bones; but it is uncertain whether they also form the hinder boundary of that aperture by extending round it, as in *Sphenodon*, or whether basipterygoid processes of the basisphenoid complete it posteriorly, as in certain Lizards. Four longitudinal ridges run along the palate; two of these, near the middle line, start from the front of the pterygoid foramen and, passing almost directly forwards, extend between the narial openings, possibly on to the vomers, but their anterior terminations are indistinct. About 15 millims. of the anterior part of the right ridge widens somewhat and is deeply pitted, leading to the conclusion that it supported one or more rows of teeth; but there is nothing to show that the hinder part of this ridge was provided with a dental armature. The left ridge does not show these parts so distinctly. The other two palatal ridges are seen outside the first pair, and starting from very nearly the same point; they curve outwards and forwards, terminating a little behind the nasal openings: it is uncertain whether they supported teeth.

The Base of the Cranium is extremely long and narrow, and is one of the striking peculiarities of the skull. I have succeeded in exposing it throughout its length, but the result is not altogether satisfactory, for the occipital articulation is not shown, and there are no indications of subdivisions. Its greatest length from the hinder end to the truncation of the presphenoid is about 70 millims.; its greatest width appears to have been in the region of the condyle, and could not have been more than 12 millims. The hinder third, which I regard as the basioccipital, is deeply grooved longitudinally on the under surface, the sides of the groove forming each a lateral phalange, with a rounded thickening anteriorly and posteriorly. The sides of the bone are also deeply concave, and the upper surface, which forms the floor of the brain-case, is likewise concave from end to end, but V-shaped from side to side. The hinder end of the basioccipital is deeper than it is wide, but unfortunately the articular surface is destroyed. The absence of thickening at the sides of the foramen magnum shows that the articular surface was altogether below the foramen, and I conclude, therefore, that it was single and median; and, further, if the vertebræ with only slightly ossified centra, described at p. 489, belonged to this type of Reptile, then in all probability this occipital articulation was similarly deeply hollowed, and more so than in *Pareiasaurus*, which would possibly account for its imperfect preservation. On the middle third of the cranial base, or basisphenoid region, the groove of the lower surface is gradually lost as it approaches the pterygoid foramen; a ridge on each side runs obliquely downwards and forwards, and is continuous with the bone forming the side wall of the pterygoid foramen. These two ridges doubtless form the basipterygoid processes of the sphenoid; and, seeing that the quadrate processes of the pterygoids arise from the sides of the pterygoid foramen, the basipterygoid processes could not have been long, and may have been entirely excluded from the foramen by the meeting of the pterygoids behind it. Above the lateral ridge the basisphenoid passes upwards and forwards on each side, but the extent of these lateral wings is not seen, and it is uncertain whether they are continuous with the cranial roof. From their position these wings would appear to be alisphenoids, and this seems to be confirmed by the occurrence of a large foramen on each side, just in front of their upper ends, which probably gave exit to the optic nerves. A short distance in front of these foramina the base of the skull is much reduced in size, and is truncated anteriorly; this appears to be the presphenoid, and above it is a trough-like bone, occupying the position of a pair of orbitosphenoids, which joins the frontals above, and for part of its length is grooved below. A cartilaginous ethmo-vomerine septum doubtless extended forwards from the presphenoid, with its upper edge lodged in the groove below the cranial floor. The lower part of this septum was ossified for some distance above the floor of the nasal chambers, but to what extent cannot be seen.

Immediately above the front of the presphenoid is the pineal fossa, and directly below it the pterygoid foramen. In the basioccipital region the side walls of the brain-case are continuous with the base and roof, but to what extent they are formed by the exoccipitals cannot be seen, neither is it certain to what extent the supraoccipital enters into the formation of the roof. The brain cavity is high and long, but in all probability only a small part of it was occupied by the brain.

The Back of the Skull (Plate 40) is remarkable for its extreme width in proportion to the size of the head, for, without the horns or spines, it measures more than 6 inches (155 millims.) across the quadrate region, the height being only 3½ inches (90 millims.). The hinder end of the basioccipital being mutilated, its form is unknown; but it is certain that, with the exception of the slightly enlarged ends of the lateral phalanges mentioned above, there are no paroccipital processes. The foramen magnum is wider than it is high, only half of it being shown in the figure, and it is broader above than below; indeed, it forms nearly a semicircle, with the curve downwards. Attention has already been directed to the supraoccipital crest connecting the roof of the brain-case with the outer plates of the skull, and to the probability that the two median outer plates (*s.o.*) are expanded portions of the same bone. The uncertainty as to what bones roof over the brain-case, and surround the foramen magnum, has also been alluded to; there can be no doubt, however, that the side wall of the foramen is formed by the exoccipital, which at the upper angle gives off the broad horizontal buttress, and this, arching very slightly upwards and outwards, abuts upon the outer wall, or cheek, at the junction of the bones I have referred to as supra-temporal and epiotic. This buttress is doubtless in part formed by the opisthotic, although the extent of the latter is uncertain; there is, however, an oblique ridge on the under side, a little way from the brain-case, which may indicate the junction of the exoccipital and opisthotic, in which case the latter bone would form by far the greater part of the buttress, as it does in Lizards.

As a consequence of the great length of the base of the skull, the origin of the quadrate process of the pterygoid is placed far underneath, and, although it passes somewhat backwards to the quadrate, it is necessary to look at the occiput, partly from below, in order to see these parts at all satisfactorily (Plate 40). In this view, the pterygoid is seen to have a considerable vertical extent, and its process, after curving outwards and backwards for about 30 millims., is united with the cheek bones, but its lower part may be followed until close to the quadrate articulation (*qu.*), which is very near the lower and outer angle of the occiput, and the strong spine, here situated, may be part of that bone, as may also a portion of the inner wall of the cheek (*qu.* ?) below the supra-temporal. The last-named bone bears a large spine on its hinder margin, and above is in close relation with the epiotic, which bears one of the largest horns of the skull, just where it joins the opisthotic buttress. Above this buttress is the upper post-temporal fossa, roofed over by the supra-occipital. There being no process extending from the basi or exoccipital bone to the quadrate, as there is in Dicynodonts, the lower post-temporal fossa is widely open below, as it is in most Lizards.

The space above the quadrate process of the pterygoid (*pt.*) opens freely into the orbit, but it is partly separated by a broad thin vertical bar of bone, which extends upwards from the pterygoid and joins the prootic or parietal, or perhaps both, and about its middle gives off a broad process, tapering inwards to a point. This vertical bar occupies much the same position as the columella of the Lizard skull, but whether it is the homologue of that bone or a part of the otic capsule, I am unable to say. The *foramen ovale* was probably situated a little above the point of the inward process.

The *Horns* of this Reptile are developed to such a remarkable extent as to call for a more detailed description than has yet been accorded them. In their present condition many of the horns are imperfect, but it is evident that when complete, most of them were somewhat flattened and sharp pointed, the exceptions being the rounded interparietal boss, and the two or three small knobs on each side of the parietal region. The lateral maxillary horns, also, are rounder than most of the others.

The largest pair of horns, or horn-cores as they should be more properly termed, are those at the hinder and outer angle of the upper surface (Plate 38), which are supported by the epiotics, and, being curved outwards and backwards, give quite a bovine appearance to the head. The right horn is a little longer than the left, and, with the pedicle which supports it, is rather more than 3 inches (60 millims.) in length. In section, this horn is nearly semicircular at the base, but becomes round towards the extremity. The rounded surface looks downwards and forwards, while the flattened side looks upwards and backwards, the two surfaces meeting so as to form a distinct anterior and posterior edge. The surface of this horn is marked by indistinct longitudinal ridges and striations forming a comparatively smooth surface, which ceases suddenly at the base, and is at once succeeded by the deeply-pitted surface of the pedicle. All the horns and bosses have a similar smoothness ending abruptly at the base. The upper edge of the pedicle bears a short spine (12 millims.) which may be an outgrowth of the squamosal bone. Two spines extend backwards from the hinder margin of the cheek (Plate 37), each about an inch long (25 millims.). The upper one is much flattened, and is supported by the supra-temporal bone, which also bears a smaller spine upon the outer surface, unless, as is quite possible, this spine is part of the prootic element. The lower spine of the hinder margin is thick, curved, and triangular in section, the angles being keen; it may belong to the quadrate or to the quadrato-jugal. The last-named bone bears an outwardly-directed spine, about the same length as the two just described, but more sharply pointed and flattened, with two sharp edges. Below this there are two small prominences close to the articulation for the lower jaw, which may be part of this bone or of the quadrate. The jugal and maxilla each bear an outwardly-projecting spine, which, when perfect, was probably not so long as that of the quadrato-jugal. The jugal spine is flattened and situated near the hinder and lower corner of the orbit, while that of the maxilla is rounded and placed just behind the nasal aperture.

The nasal bones carry each a stout but flattened horn, which, when perfect, could have been but little less than that of the quadrato-jugal. Of the three spines overhanging the orbit, the hinder one is the largest, and probably belongs to the postfrontal bone, while the anterior one most likely represents the prefrontal.

On the upper surface of the skull (Plate 38), commencing at the back, we find the supraoccipitals carrying a pair of prominent horns near their hinder margin; these are somewhat flattened and curved forwards, when perfect they must have been nearly an inch in length. Each of the supraoccipitals also bears one or two small bosses in front of the larger horns. On each side of the pineal fossa there is a spine, evidently upon the parietal bone, and behind this a small boss. More anteriorly the frontals carry a pair of spines. In the interparietal region there is a rounded prominence occupying the middle of the area which I have called an intercalary bone, and evidently carried a median horn.

The small raised and flattened space between and behind the bases of the nasal horns may also be the remains of a small median spine, and with this the total number of horns, spines, and bosses on the outer surface of this skull is forty.

The character of the surface of these horns, and the sharp line of demarcation between it and the pitted bone at the base, even in the case of the small bosses, makes it tolerably certain that they were ensheathed in a special horny covering, distinct from the epidermis which covered the general surface of the bones.

With the exception of the premaxillaries and post-orbitals, every bone of the exterior of this skull bears, at least, one horn, and this is so marked a character that, it seems at first sight, every horn must represent a distinct bone; but, besides the extra small bosses seen upon the supraoccipitals and parietals, there are two small extra spines which seem to belong to the quadrato-jugal. The smooth surface of the premaxillary bones may be an indication of their covering having been of a more horny nature than the general epidermal covering of the pitted bones.

Dentition.—The teeth being small, there was at first some difficulty in knowing whether the creature possessed any; however, little by little, portions of the dental margin were uncovered, so that now, although teeth are only seen on one side, the entire dentition of the upper jaws is well known, and the close resemblance, in nearly every particular, to the form and arrangement of the teeth in the living *Iguana* is very striking.

The margin of the jaw when seen from below (Plate 39) must, before its distortion, have been nearly semicircular, and short in comparison with the size of the skull. The measurement around the arc of the semicircle is about 110 millims., and the chord of the arc at the hindermost teeth about 70 millims. The edges of the premaxillæ and maxillæ are thin, and on the inner side slant outwards and form a parapet with a ledge raised a little above the general level of the palate. The inner aspect of this parapet is marked by slight vertical depressions corresponding to each tooth, shown best on the left side, but not visible in the figure. The teeth are set on this parapet in a thoroughly typical pleurodont fashion. There are spaces for about twelve teeth on each side, and on the right eight can be traced still in place (Plate 37, fig. 2); spaces for the other four are left, the teeth having fallen out, possibly during the life of the animal, in the natural process of renewing the dentition, or the loss may have been due to post-mortem injury. The hindermost teeth are a little smaller than the others. In the side view of the skull (Plate 37, fig. 1) the whole dentition of the right side has been restored in outline.

Each tooth consists of a long fang surmounted by an enlarged somewhat spatulate crown. This crown is flattened on the inner side (Plate 37, fig. 4), and marked by a series of seven or eight slightly radiating ridges which extend over a large part of this surface to the outer edge. The outer part of the crown (fig. 3) is rounded and marked towards the edges by crenulations which, meeting those of the inner side, form the serration with which the edges of these teeth are provided. The exact form of the crowns of these teeth is not easy to make out, owing to the coarse matrix; but there is really more detail to be seen than might have been expected, and the enlarged and restored figures on Plate 37 (figs. 3, 4) give a fairly correct idea of the form of one of the middle teeth of the left side. The crown is seen to be subpentagonal in outline, the base being its attachment to the fang, from this the slightly curved and non-serrated sides rise a little more than half way towards the apex where the two serrated edges meet at an obtuse angle. The outer surface has a more oval appearance than the inner owing to its being more inflated. Some of the teeth have shorter crowns, possibly due to wearing.

A study of the different parts of the parapet and dental series shows that each tooth lay against the parapet in a slight depression, the base resting on the step, and became fixed to the parapet by a bony deposit; so that at the margin the bone is seen passing a little way inwards between the teeth. In some places the teeth have been forcibly broken away, leaving a portion of the fang still cemented to the parapet. One of the fangs shows a slight depression at the lower part, apparently indicating absorption by the pressure of a young tooth, such as takes place in *Iguana* and other Lizards. As a matter of fact the dentition of this specimen agrees so closely with that of *Iguana* that the above description would answer equally well for the one or the other, the only differences between the two being that the teeth of the present specimen are proportionately larger and fewer in number, there being only twelve on each side, while *Iguana* has double that number, and the crowns are less pointed and have no median ridge. Allusion has already been made to the ridges along the palate, and to the probability of some of them at least having supported teeth. There will be occasion to speak of this again when considering the affinities of this unique Reptile.

Affinities.

The extreme development of horns on this Elgin skull reminds one forcibly of the Australian *Moloch* and the American *Phrynosoma*, but although the Elgin Reptile undoubtedly possesses several important Lacertilian characters, and apparently finds its nearest living allies in that group, yet it presents peculiarities of structure which prevents its being referred to the Lacertilia. The anterior position of the posterior nares, which open directly upwards into the nasal chambers; the character of the opisthotic and exoccipital process, forming a strong buttress extending to the base of the pedicle for the lower jaw, as well as the mode of dentition, are characteristically Lacertilian. On the other hand, the meeting of the pterygoids on the palate in front of the pterygoid foramen and base of the skull, as well as the presence of a lower temporal bar, are characters not met with among the true Lacertilia; nevertheless, the pterygoids come very near together in *Iguana*, and in *Sphenodon* they are close together both before and behind the foramen, but are said not to unite. *Sphenodon* also has a complete lower temporal bar. Certain Lacertilia have the supra-temporal fossa covered in by bone, but there being no lower arcade the cheeks are uncovered.

The complete covering in of the upper and side walls of the Elgin skull gives it some resemblance to that of a Chelonian, more especially as they both have the lower arcade complete; but the epiotics and paired supraoccipitals, which form part of the outer wall in this fossil, are not present on the surface of the Chelonian skull; and further, although the pterygoids meet in front of the base of the skull in Chelonians, they have no pterygoid foramen or distinct quadrate process; besides this the Chelonian posterior nares are thrown farther back by the arching over of the palatines, as we have seen they are in Dicynodonts.

The pitting of the exterior of this skull is very like that of a Crocodile, but in matters of structure the two are wide apart.

I am not aware of any recent form that makes a near approach to this Elgin skull, although I believe it presents very strong Lacertilian affinities. It is quite unlike any of the Reptiles which have hitherto been described from the Elgin sandstone; indeed, with the exception of the *Pareiasaurus* to be presently noticed, I know of no fossil that it at all resembles.

The Amphibians (Stegocephala) and lowly Reptiles (Proganosauria) recently described by Dr. CREDNER (9), from the Permian of Saxony, have only a very distant relationship to this Elgin Reptile.

When seeking for allies of this fossil among extinct forms, one is naturally led to examine such as have been found elsewhere similarly associated with Dicynodont remains. With the Dicynodonts and Theriodonts described by Sir R. OWEN in his classical work on the South African Reptiles (38), occurs the very aberrant form named *Pareiasaurus,* two species of which were described, *P. bombidens* and *P. serridens.* The two skulls of these are unfortunately in a bad state of preservation, but the uniform series of teeth, so unlike those of the Theriodonts, seemed to indicate a possible affinity with the Elgin fossil, and this was rendered more probable when comparison was made with another example, described by Professor SEELEY (41), showing a sculptured exterior to the skull, in which also the arrangement of the bones agreed fairly well with the Elgin specimen, although there were no horns. The palate of Professor SEELEY's specimen, which he referred to *P. bombidens,* is not sufficiently exposed for comparison (41, Plate 15), and on turning to the palate of *P. serridens,* which he also figures (41, Plate 16), the differences between it and the Elgin form appeared to be too great for any possibility of affinity. Whether these differences are due to the imperfections of this example of *P. serridens,* or to its belonging to another genus of Reptiles, has yet to be decided; but another South African skeleton, obtained by Professor SEELEY, and named by him *Pareiasaurus Bainii* (44), has the palate well exposed, and it agrees very closely indeed with that of the Elgin skull, and is quite unlike that of *P. serridens.* This latest acquisition from South Africa has been described by Professor SEELEY before the Royal Society (44). The skull is about 18 inches long, and, therefore, nearly three times the length of that from Elgin, and is proportionately flatter; there are no indications of horns, but the outer surface of the bones is similarly ornamented, and their general arrangement seems to be very much the same, while the structure of the palate and the mode of dentition, are so far alike, that I am convinced the two are allied forms, although the differences between them may be of more than generic importance. Seen from behind the two skulls are found to have similar post-temporal fossæ divided in each by a plate arising from the roof of the brain-case, and supporting the outer plates of the skull; there is a similar exoccipital and opisthotic buttress arising from the upper part of the foramen magnum; but in *Pareiasaurus* this buttress is more ponderous and turns more downwards than it does in the Elgin skull. The quadrate process of the pterygoid is similarly placed far forwards and consequently there is a similar deep recess where the foramen ovale seems to have been placed. The basioccipital has a pair of tubercles on the lower part, but, like the Elgin specimen, has no process extending towards the quadrate. Seen from below the palates are remarkably alike, the teeth form a similarly uniform series, and so far as I can see, in both are of the pleurodont type. The anterior palatal apertures are in both placed near the front and open directly upwards; there are similar triangular spaces in front of the quadrate process of the pterygoid with a like projection from the inner side. *Pareiasaurus* has six ridges on the palate, each apparently carrying a double row of teeth. Two of these rows seem to be on the vomers and are far forwards between the fore part of the inner nasal openings; in the Elgin skull this part is obscured, and it is therefore uncertain whether any such vomerine ridges were present. A second pair runs backwards in *Pareiasaurus*, from between the palatal openings to end close to the pterygoid foramen, corresponding with the median ridges in the Elgin fossils, which in part at least appear to have carried teeth. The third pair in *Pareiasaurus* starting from the outer side of the nasal opening extends backwards and inwards to end very near the inner pair, and corresponds with the outer pair in the Elgin skull which are placed behind the nasal apertures, but show no signs of having had teeth. There is a pterygoid foramen just behind the palatal ridges, in both specimens, which has much the appearance of the posterior nares of a Mammal, but cannot, I think, be in any way of an homologous nature. Behind this foramen the bases of the two skulls have a different appearance on account of the extreme length of the base in the Elgin specimen, and its shortness and stoutness in *Pareiasaurus*.

When we turn to the upper part of the skulls, there is again a close resemblance between them. In both the nostrils are double; there is a lower temporal arcade, the lateral temporal fossæ are covered in by bone, the surfaces of the bones are deeply sculptured, and the arrangement of the bones of the exterior seems to be the same in principle. It is very evident, from their close resemblance in so many important points of structure, that these two forms are related; but, at the same time, there are differences which suffice to separate them, at least generically. In the first place, there is the remarkable development of horns in the Elgin fossil, which is not found in *Pareiasaurus*, although there are one or two protuberances on the hinder border; and there is also the extreme proportionate length of the base of the skull, and possibly the presence of an interparietal bone is peculiar to the former. Although the teeth of *Pareiasaurus* are said to be implanted in sockets, while those of the Elgin skull are distinctly pleurodont, yet I venture to think that the section figured by Professor SEELEY (41, Plate 16), showing bony matter between the teeth, is not conclusive evidence of distinct sockets. *Pareiasaurus* is not only much larger than the Elgin reptile, but its skull is broader proportionately and more depressed.

Having come to the conclusion that the nearest ally of this Elgin reptile is *Pareiasaurus*, it remains to be seen what the relationship of these forms may be to other groups of Reptiles. This has been considered by Professor SEELEY, with regard to

Pareiasaurus, and he has had a very large part of the skeleton besides the skull to deal with. In the present instance we have only the skull as a guide, but it may be well to see how far it confirms the opinions expressed by Professor SEELEY, who, speaking of the exterior of the skull of *Pareiasaurus*, says it agrees with Labyrinthodonts in five points, which, put briefly, are:—(1) in form; (2) sculpture of cranial bones; (3) arrangement of these bones; (4) presence of mucous canals; (5) absence of lachrymal bone from the corner of the orbit. The first three of these points are likewise found in the Elgin skull, but there is no evidence of mucous canals, and the fact that there is an opening from the orbit to the nasal chamber, makes it hazardous to say there was no lachrymal bone. The development of the epiotics to form prominent angles at the back of the skull, is another Labyrinthodont character, found in both forms, which should be noticed.

The large size and approximation of the external nares are regarded by Professor SEELEY as a reptilian character of *Pareiasaurus*, and this peculiarity is found also in the Elgin skull.

In so far, then, as regards the exterior of the skull, both these fossils show an affinity with Labyrinthodonts rather than with Reptiles.

We now come to consider the palate, and, from what has been said above, it will be agreed, I think, that the later specimen described by Professor SEELEY (44), is constructed upon precisely the same plan as that of our Elgin fossil, and the Professor's account of its constituent bones, so far as they can be traced, in no way invalidates this agreement; but, although we are agreed as to the probable arrangement of the bones, I find myself unable to accept his interpretation of the apertures of the palate. He regards the interpterygoid vacuity, or foramen, as the true posterior nares, while the anterior openings of the palate, he speaks of as merely "palatal vacuities," and, at p. 317, says, "This structure of palate is best compared to the condition in Mammals, though approximated to in Rhynchocephalia, Teleosauria, &c.," although, on p. 332, the palate is said to be "better compared with that in Lizards and *Sphenodon*."

I have already expressed the opinion that this form of palate has the very closest resemblance to that of a Lizard, and, if compared with that of *Iguana* or *Sphenodon*, there will be found to be a most striking similarity, part for part. It is true that in the former, the pterygoids do not meet in the middle line, but they approximate very closely; and, in the latter, they meet in the middle, although they are said not to unite. The union of the pterygoids in the middle line, however, is a common Reptilian character, but one that is rare among the Mammalia, for in the latter, with few exceptions, the palatines form the front boundary of the posterior nares.

I see no more reason for regarding the pterygoid vacuities of *Pareiasaurus* as posterior nares, than for giving a similar interpretation to the corresponding vacuities of *Iguana* or *Sphenodon*. In mammals, the posterior nares certainly communicate with the space above the palate, which forms the nasal chambers, and in the Elgin skull these apertures also open directly into the orbito-temporal spaces above the palate, but there is no evidence of any bony passages leading to the nasal chambers. It is true the connection may have been by membranous or cartilaginous channels, but this is only begging the question; and in the absence of more definite evidence than is at present forthcoming, I feel compelled to regard the anterior palatine apertures as the posterior nares, and, consequently, the palates of *Pareiasaurus* and of the Elgin fossil present, to me, Lacertilian rather than Mammalian affinities.

I fail to find anything in the structure of this Elgin skull showing affinities with either Dicynodonts or Theriodonts; but Professor SEELEY sees in certain parts of the skeleton of *Pareiasaurus* a resemblance to the Anomodontia, and thinks the genus more nearly related to that group than to any other order of the animal kingdom.

There can be no doubt that in whatever group the new specimen of *Pareiasaurus* finds its resting place, thither this Elgin fossil will have to follow, and, for the present, will remain in the same family as an aberrant group of the Reptilia, possibly allied by its trunk skeleton to the order Anomodontia, understood in its wider sense. The necessity for the establishment of a new genus and species for the reception of this Reptile is obvious; it will be distinguished from *Pareiasaurus* by the large development of horns and spines, by the elongated base of the skull, by the different form of the teeth, apparently by the absence of mucous canals, and probably by the presence of an interparietal or intercalary bone. It is proposed to name this specimen, after the district where it was found, and in allusion to its remarkable form, *Elginia mirabilis.*

10. NOTE ON A SACRUM AND SOME VERTEBRÆ (Plate 41).

The Elgin Museum and the Geological Survey possess, each a specimen from the Elgin Sandstone containing impressions of vertebræ, which are believed to come from Cuttie's Hillock Quarry, but on this point there is a little uncertainty. A cast taken from the Elgin Museum example shows six consecutive vertebræ, four of which are sacral, and two presacral, while the Survey specimen, which may be part of the same skeleton, contains the impressions of two late dorsal, or lumbar, vertebræ. The last-named vertebræ show the left side, as well as the anterior and posterior faces; but the neural spines are only represented by the impression of an anterior and of a posterior extremity (figs. 1–3).

These vertebræ are a little distorted: each centrum is about 28 millims. long and 18 millims. wide at its expanded extremities, but in the middle it is pinched in, being only about 8 millims. wide at this part. That these centra were formed by a mere film of bone surrounding the persistent notochord was amply testified by the fact that one of them, when it came to me, had the notochordal space completely filled with the sandy matrix, and the space left by the dissolving away of the bone was not thicker than a stout piece of paper. Unfortunately, it was found necessary to remove this mould of the notochord before a cast could be taken. The pre- and post-zygapophyses are large, strong, and widely expanded, being at least 58 millims. across (fig. 2), they are supported by buttresses rising from the neural arches, and almost wholly above the neural canal. The neural spines are incomplete, but the greatest height of the most complete vertebra, in its present condition, is about 55 millims. The posterior end of the centrum is nearly circular and 17 millims. in diameter; the oval neural canal is 8 millims. high; from the neural canal to the base of the spine is about 13 millims., and about 17 millims. of the spine are preserved, but, judging from the other specimens, this must have been about 22 or 24 millims. when perfect. Immediately above the neural canal is a lenticular area, the middle of which forms an elongated projection with the under surface marked by strong antero-posterior grooves, as if for the attachment of ligaments. This projection may have been received into a corresponding depression in the succeeding vertebra, but in neither of the specimens is the anterior face of a vertebra sufficiently well preserved to show this clearly. In a side view the post-zygapophysis is seen to extend beyond the centrum, and to form a flattened articular surface looking almost directly downwards; it reaches upwards to the base of the neural spine, and as a prominent arched bar passes nearly to the front of the vertebra.

From the front part of the neural arch a process passes upwards, outwards, and a little forwards to form the pre-zygapophysis, the articular face of which looks almost directly upwards. This process also is supported by a buttress rising from the neural arch in front of and below the post-zygapophysial bar, which, passing forwards, lies below, and is connate with the pre-zygapophysis; it is a transverse process with only the extremity free, and this, a little enlarged, terminates in a slightly depressed surface which looks somewhat forwards, and may possibly have supported a small rib. It is quite possible that these two vertebræ may have belonged to the same individual as those to be next described, and, if so, could not have occupied a position much in advance of the two pre-sacral vertebræ at the front of that specimen, the anterior vertebra of which has the transverse process in almost the same position.

The Elgin Museum specimen (figs. 4, 5) has the left side of the vertebræ deep in the matrix, but the casts prepared from this, and from the pieces of stone which have been broken off, show the right side nearly complete, with parts of the left side. All the vertebræ are somewhat distorted, but fortunately the exposed right side is the most perfect, and allows their forms to be very well made out. The right side of the centrum of the most anterior vertebra, and parts of the neural arches of both presacral vertebræ, are wanting, but the form of these parts is, to a large extent, supplied by the left side. The two presacral vertebræ closely resemble the two more anterior ones above described, and the centra are likewise about 28 millims. long. The neural spines are preserved, and the anterior one stands 36 millims. above the neural canal; it is flattened from side to side, and at its summit seems to have been about 15 millims.

from front to back, while below it reaches further backwards. The second vertebra has the summit of the spine extended laterally. The post-zygapophyses of these two vertebræ have the same arched form as in the more anterior vertebræ of the other specimen, but the pre-zygapophyses and their connate transverse processes are becoming modified. In the front one the difference is only slight; the articular surface remains much the same, but the transverse process is more prominent, and has receded somewhat. The hindmost of the pre-sacral vertebræ has the pre-zygapophysis enlarged, and extending further down upon the side of the vertebra, while the transverse process is also much stouter, has receded still further, and its termination has become expanded to form a heart-shaped cup, directed backwards, apparently for the attachment of a rib.

The four hindermost vertebræ of this series are very different from those in front of them, and evidently form the sacrum; they all seem to be firmly ankylosed together, although the centrum of the anterior one is more clearly defined from the one which follows it than the hinder three are from each other. The neural arches are not well shown on either side, and the obliteration of the zygapophysial articulations may be more apparent than real, but it is quite certain they were unlike those of the pre-sacral vertebræ.

The anterior sacral vertebra has a very peculiar form; the under surface of the centrum, which is about 28 millims. long, instead of being keeled, like those preceding it, is concave from side to side as well as from back to front; it is slightly expanded anteriorly, where it articulates with the next vertebra, but widens out posteriorly, so as to form a broad triangle, each hinder angle of which extends outwards into the large buttress-like sacral rib, and this, curving backwards, becomes expanded vertically, and reaches beyond the middle of the fourth sacral centrum, thus enclosing a deep semi-oval space, widest posteriorly. The junction of this sacral rib with the vertebra is, probably, indicated by the oblique ridge passing forwards and outwards from the hinder margin of this centrum. Viewed somewhat more from the side, the pre-zygapophysis is seen to be much expanded, and, extending backwards, is apparently continuous with the transverse process and large sacral rib, no division between it and the transverse process being visible, but together they form a wide slightly concave surface. A side view shows the articular surface of the pre-zygapophysis to be directed somewhat forwards as well as upwards. Opposite the space between the first and second sacral ribs, as seen on the upper surface, there is a wedge-shaped prominence, probably marking the proximal end of the sacral rib, which is seen to form a deep trough, with a wide but thin inner and upper side, evidently for the reception and support of the ilium. The neural spine of this vertebra has a greater antero-posterior extent than those which succeed it, and resembles in this respect the two immediately in front of it, but is directed a little backwards.

The three hinder sacral vertebræ are much alike in form (fig. 4) but very different from the anterior one. In the first place they are much shorter than the front one, and decrease in size towards the hinder extremity; the centra are respectively 20 millims., 18 millims., and 17 millims. in length. One side of these centra being crushed, the form of their under surfaces is not very clearly shown, but they were evidently narrow below, and seemingly almost keeled. Their sides are a little concave from before backwards, and convex from above downwards, the union of their articular faces being marked by roughened ridges. From each centrum a transverse process passes upwards as a flying buttress, and is continuous with one of the irregular processes, which are seen, on the upper surface, extending outwards and backwards from the region of the apparently fused neural arches. Each of these processes terminates in an expanded and roughened end, and this, as well as the gradual increase in length of the hinder processes, makes it evident that they came in contact with the ilium and thus fulfilled the function of true sacral vertebræ. The neural spines of these vertebræ are expanded laterally at their extremities and the hinder ones are closer together.

Can these vertebræ be referred to any one of the genera which have been found in the Elgin sandstone? This is a question which will naturally be asked, but cannot be so easily answered. In the first place, *Stagonolepis, Hyperodapedon*, and *Telerpeton*, may be dismissed, as their vertebræ are quite unlike, and we have therefore only to consider the forms from Cuttie's Hillock. The remains of vertebræ on specimen No. 3, *Gordonia Duffiana*, do not allow a close comparison to be made; but certainly, unless the forms of those of the dorsal region, as shown by the casts (Plate 32, figs. 4, 5), are very deceptive, they are quite unlike any of those now under consideration. The circular impression seen in the same slab (Plate 31), which may be the cast of the end of a vertebral centrum, is just such as would be made by one of the centra of the present specimens, and possibly indicates a similar condition of ossification, but there are no sufficient grounds for referring them to the same genus.

The caudal vertebræ (specimen No. 6, Plate 33, fig. 5) have their anterior and posterior end about equally wide and thus resemble the present vertebræ, but the utmost that can be said is that they might possibly have belonged to a similar but much smaller animal.

None of the vertebræ referred to Dicynodonts by Sir R. Owen (38), Professor Huxley (16), Mr. Lydekker (21), or Professor Seeley (43) at all resemble these specimens in form, and in none of them does there appear to be a similar condition of ossification of the centra.

The sacrum referred by Sir R. Owen to *Dicynodon tigriceps* (38, Plate 36) has a large sacral rib somewhat like that now described, but the sacral centra are all similar in form, and therefore quite unlike those of the present specimen.

In so far as the vertebræ of Dicynodonts are known, they differ so much from the present specimens as to prevent the reference of the latter to the Dicynodontia.

The genus from Cuttie's Hillock remaining to be considered is *Elginia*, of which only the skull is known, but as its nearest ally *Pareiasaurus* has much of the skeleton preserved, including sacral and other vertebræ, a comparison of these with the Elgin vertebræ may show what probability there is of these vertebræ belonging to *Elginia. Pareiasaurus* has a large sacral rib (43, Plate 12) very similar to that in the sacrum referred by Sir R. OWEN to *Dicynodon tigriceps*, and supporting the ilium in much the same way as must have been the case in the present specimen. The vertebræ of *Pareiasaurus*, when seen from above, show a somewhat similar arching of the post-zygapophysial bars, but in other respects there are great differences between the two. In *Pareiasaurus* the vertebral centra are shorter and broader, the neural spines are rounded and knob-like, the sacrum is said to be formed of two ankylosed vertebræ only, and these are not unlike those before and behind them. It is possible that some of the vertebræ behind these two sacrals may have had transverse processes reaching to the ilium, but their centra were not ankylosed to each other. It will at once be seen that in the present specimen, the widened anterior sacral vertebra and the three narrow posterior ones all fixed together, constitute a sacrum quite unlike that of *Pareiasaurus*. It would be very hazardous, therefore, in the absence of definite evidence, to refer the present sacrum and vertebræ to *Elginia;* nevertheless, it is possible that they may have belonged to a form related to *Pareiasaurus*, such as *Elginia;* and the differences between this sacrum and that of *Pareiasaurus* may be consistent with the distant relationship, which seems to be indicated by the similarities and differences observable in the skulls of these two genera.

III.—THE STRATIGRAPHICAL POSITION OF THE ELGIN SANDSTONES.

When Reptiles of Mesozoic character were found in the sandstones at certain localities near Elgin, these rocks, which had previously all been referred to the Old Red Sandstone, were acknowledged to be of two distinct ages; but the relation of the reptiliferous beds to those containing undoubted Old Red Sandstone Fishes was left uncertain, no section being known in which both series of beds were seen. The opening of the quarry at Cuttie's Hillock exposed the section already noticed (p. 434), wherein the age of the rocks is satisfactorily proved by fossil evidence, Reptilian remains occurring above a pebbly layer, while below that band a large Fish has been obtained, which has been determined by Dr. TRAQUAIR to be the characteristic Upper Old Red Sandstone form, *Holoptychius nobilissimus*.

The opinion expressed by Professor HUXLEY in 1859 (12) that the palæontological evidence showed the reptiliferous sandstones of Elgin to be of Mesozoic rather than of Palæozoic age, has been abundantly confirmed by more recent discoveries, the chief of which have been made known by the Professor himself; and in his paper on *Hyperodapedon*, published in 1869 (15), he fully discussed the significance of the Elgin Reptiles, as pointing to the Mesozoic age of the strata in which they were found.

Until the discovery of Dicynodont remains near Elgin this group of Reptiles was only known from the Beaufort and Stormberg group, of the Karoo formation, in South Africa, and in strata of approximately the same age in India, the Panchet beds of the Gondwanas. M. TRAUTSCHOLD (46) has described specimens from Permian beds at Kasan, which he refers to the genus *Oudenodon*, but it seems somewhat doubtful whether such fragmentary specimens, as are represented by his figures, can be identified with certainty.

It is worthy of notice that the Reptiles found at Cuttie's Hillock are altogether different from those which have been met with at other localities near Elgin; thus, from Lossiemouth, we have *Stagonolepis*, *Hyperodapedon*, and *Telerpeton;* from Spynie, *Hyperodapedon*, *Telerpeton*, and a *Ceratodus*-like Fish tooth allied to *Sagenodus;* and from Findrassie, *Stagonolepis* and *Dasygnathus*. From Cuttie's Hillock, on the other hand, have been obtained two forms of Dicynodonts, *Gordonia* and *Geikia*, accompanied by *Elginia*, an extreme type of Reptile allied to the South African *Pareiasaurus*.

The Elgin Reptiles, it will be seen, form a very similar series to those which occur in the Gondwana beds of India (3 and 21), where *Hyperodapedon*, *Parasuchus* (allied to *Stagonolepis*), Dicynodonts, and Labyrinthodonts have been found; and there also the Dicynodonts do not occur at the same locality as *Hyperodapedon* and *Parasuchus*, the former being found in the Panchet rocks, which are referred by Dr. BLANDFORD (3) to a lower horizon than the Kota Maleri beds, where the *Hyperodapedon* and *Parasuchus* have been met with.

If the Elgin Reptiles be compared with those from the South African Karoo beds, we see that it is those from the Cuttie's Hillock Sandstone which find their counterparts in the Beaufort and Stormberg beds. The two types of Dicynodonts, *Gordonia* and *Geikia*, from Cuttie's Hillock are very similar to the *Dicynodon* and *Ptychognathus* of South Africa, while *Elginia*, as we have seen, finds its nearest ally in *Pareiasaurus*.

The correspondence which is found to exist between the Reptiles of the Elgin Sandstones and those from the Indian Gondwanas, and the South African Karoo beds, as well as the absence from each of these localities of types which might be expected to occur, leads to the inference that in each country new forms of Reptiles await discovery. The Karoo beds of South Africa may yield Crocodilia; the discovery of Pareiasauria and Theriodontia may be anticipated in the Gondwanas of India; while Labyrinthodontia and Theriodontia may be expected from the reptiliferous Elgin Sandstones.

IV.—LIST OF WORKS CONSULTED.

1. Agassiz, L. *Stagonolepis Robertstoni.* Poissons Fossiles, V. G. R., p. 139, Pl. 31, figs. 13, 14; 1844.
2. Bain, A. G. On the Discovery of the Fossil Remains of a Bidental and other Reptiles in South Africa. Trans. Geol. Soc., ser. 2, vol. 7, pp. 53 and 175; 1845–56.
3. Blanford, W. T., and H. B. Medlicott. A Manual of the Geology of India. Calcutta, 1879.
4. Beckles, S. H. On Fossil Footprints in the Sandstone at Cummingstone. Quart. Journ. Geol. Soc., vol. 15, p. 461; 1859.
5. Brickenden, L. Notice of the Discovery of Reptilian Foot-tracts and Remains in the Old Red or Devonian Strata of Moray. Quart. Journ. Geol. Soc., vol. 8, p. 97; 1852.
6. Cope, E. D. Dicynodont Reptile from Cape Colony, South Africa (*Lystrosaurus*). Proc. Amer. Phil. Soc., vol. 11, p. 419; 1870.
7. —— On the Homologies of the Cranial Bones of the Reptilia and on the systematic arrangement of the Class. Proc. Amer. Assoc. Adv. Sci. for 1870, p. 184; 1871.
8. —— On the Cranium of the Anomodontia; *ibid.*, p. 205.
9. Credner, H. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauenschen Grundes bei Dresden. Zeit. Deutsch. Geol. Gesells., I., 1881, p. 298; II., 1881, p. 574; III., 1882, p. 213; IV., 1883, p. 275; V., 1885, p. 694; VI., 1886, p. 576; VII., 1888, p. 488; VIII., 1889, p. 319; IX., 1890, p. 240; *and* Die Urvierfüssler. Naturwiss. Wochenschrift, 1891.
10. Fischer, P. Recherches sur les Reptiles Fossiles de l'Afrique Australe. Nouv. Arch. du Muséum, ser. 1, vol. 6, p. 179, Pl. 10; 1870.
11. Harkness, R. On the Reptiliferous Rocks and Footprint-bearing Strata of the North-east of Scotland. Quart. Journ. Geol. Soc., vol. 20, p. 429; 1864.
12. Huxley, T. H. On the *Stagonolepis Robertsoni* (Agassiz) of the Elgin Sandstones; and on the recently discovered Footmarks in the Sandstones of Cummingstone. Quart. Journ. Geol. Soc., vol. 15, p. 440; 1859.
13. —— On a New Species of *Dicynodon* (*D. Murrayi*) from near Colesberg, South Africa; and on the Structure of the Skull in the Dicynodont; *ibid.*, pp. 555, and 649; 1859.
14. —— On a New Specimen of *Telerpeton Elginense; ibid.*, vol. 23, p. 77; 1867.
15. —— On *Hyperodapedon; ibid.*, vol. 25, p. 138; 1869.
16. —— Vertebrate Fossils of the Panchet Rocks, Raniganj, Bengal. Palæont. Indica, ser. 4, vol. 1, part 1; 1865–1885.

17. HUXLEY, T. H. On *Stagonolepis Robertsoni* and on the Evolution of the Crocodilia. Quart. Journ. Geol. Soc., vol. 31, p. 423; 1875.
18. —— The Crocodilian Remains found in the Elgin Sandstones, with remarks on the Ichnites of Cummingstone. Memoirs Geol. Survey, Monograph III., 1877.
19. —— Further Observations upon *Hyperodapedon Gordoni.* Quart. Journ. Geol. Soc., vol. 43, p. 675; 1887.
20. JUDD, J. W. On the Relation of the Reptiliferous Sandstone of Elgin to the Upper Old Red Sandstone. Proc. Roy. Soc., vol. 39, p. 394; 1886.
21. LYDEKKER, R. Vertebrate Fossils from the Panchet Rocks, Raniganj, Bengal. Palæont. Indica, ser. 4, vol. 1, part 1; 1865–85.
22. —— Indian Pretertiary Vertebrata, *ibid.*, parts 3, 4, 5; 1879–85.
23. —— Reptilia, in Palæontology by NICHOLSON and LYDEKKER, 1889.
24. —— Dicynodontia, Cat. Foss. Rept., Amphib., Brit. Mus., part 4, p. 15; 1890.
25. —— On the Pectoral and Pelvic Girdles and Skull of the Indian Dicynodonts. Rec. Geol. Surv. India, vol. 23, p. 17; 1890.
26. MANTELL, G. A. Description of *Telerpeton Elginense*, &c., in Lower Devonian Strata of Forfarshire. Quart. Journ. Geol. Soc., vol., 8, p. 100; 1852.
27. MURCHISON, Sir R. I. On the Sandstones of Morayshire (Elgin, &c.) containing Reptilian Remains, and on their relations to the Old Red Sandstone of that Country, *ibid.*, vol. 15, p. 419; 1859.
28. —— On the Age of the Reptiliferous Sandstone of Elgin. Siluria, edit. 4, p. 267; 1867.
29. OWEN, Sir R. Description of certain Fossil Crania, &c., from South Africa (*Dicynodon*). Edinb. New Phil. Journ., vol. 39, pp. 334, 339; 1845.
30. —— Report on the Reptilian Fossils of South Africa, &c. Part 1, Description of certain Fossil Crania, &c. (*Dicynodon*). Quart. Journ. Geol. Soc., vol. 1, p. 318; 1845; and Trans. Geol. Soc., ser. 2, vol. 7, p. 59; 1845–56.
31. —— Part 2. Description of the Skull of a Large Species of *Dicynodon* (*D. tigriceps*, OWEN), &c. Quart. Journ. Geol. Soc., vol. 11, p. 532, 1855; and Trans. Geol. Soc., ser. 2, vol. 7, p. 233; 1845–56.
32. —— Part 3. On parts of the Skeleton of the Trunk of the *Dicynodon tigriceps.* Quart. Journ. Geol. Soc., vol. 11, p. 541, 1855; and Trans. Geol. Soc., ser. 2, vol. 7, p. 241; 1845–56.
33. —— On some Reptilian Fossils from South Africa. Ann. Nat. Hist., vol. 4, p. 237; 1859.
34. —— On some Reptilian Fossils from South Africa. Quart. Journ. Geol. Soc., vol. 16, p. 49; 1860.
35. —— On the Orders of Fossil and Recent Reptilia and their Distribution in Time, Rep. Brit. Assoc. for 1859, p. 153; 1860
36. —— Palæontology, 1860.

37. OWEN, Sir R. On the Dicynodont Reptilia, with a Description of some Fossil Remains brought by H.R.H. PRINCE ALFRED from South Africa, November, 1860. Proc. Roy. Soc., vol. 11, p. 583, 1860; and Phil. Trans., vol. 152, p. 455; 1862.

38. —— Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum. 4to., London, 1876.

39. —— Description of Parts of the Skeleton of an Anomodont Reptile (*Platypodosaurus robustus*, OWEN) from the Trias of Graaff Reinet, South Africa. Quart. Journ. Geol. Soc., vol. 36, p. 414; 1880.

40. PHILLIPS, J. GORDON. The Elgin Sandstones. Rep. Brit. Assoc. for 1885, p. 1023; 1886.

41. SEELEY, H. G. Researches on the Structure, Organization, and Classification of the Fossil Reptilia. Part 2. On *Pareiasaurus bombidens*, OWEN, and the significance of its Affinities, &c. Phil. Trans., vol. 179, B., p. 59; 1888.

42. —— Part 5. On Associated Bones of a Small Anomodont Reptile. *Keirognathus cordylus*, &c., *ibid.*, p. 487; 1888.

43. —— Part 6. On the Anomodont Reptilia and their Allies. Phil. Trans., vol. 180, B., p. 215; 1890.

44. —— Part 7. Further Observations on *Pareiasaurus*. Phil. Trans., vol. 183, B., p. 311; 1892.

45. TRAQUAIR, R. H. Preliminary Note on a New Fossil Reptile recently discovered at New Spynie, near Elgin. Rep. Brit. Assoc. for 1885, p. 1024; 1886.

46. TRAUTSCHOLD, H. Die Reste Permischer Reptilien des Paläontologischen Kabinets der Universität Kasan. Nouv. Mém. Soc. Imp. Nat. de Moscou, vol. 15, part 1; 1884.

47. WEITHOFER, A. Ueber einen neuen Dicynodonten (*Dicynodon simocephalus*) aus der Karoo-Formation Südafrikas. Ann. Hofmuseum Wien, vol. 3, p. 1; 1888.

48. ZITTEL, KARL A. Handbuch der Palæontologie. Palæozoologie, vol. 3, p. 556; 1889.

The following paper was received too late for insertion in its proper place. Rev. G. GORDON, LL.D. The Reptiliferous Sandstones of Elgin. Trans. Geol. Soc. Edinbr., vol. 6, p. 241; 1892.

V.—EXPLANATION OF PLATES.

All the specimens are from the Elgin Sandstone of Cuttie's Hillock Quarry, near Elgin, and the drawings, unless otherwise stated, have been made from casts of the original hollow cavities.

PLATE 26.

Gordonia Traquairi, gen. et sp. nov.

From a photograph of specimen in the possession of the Geological Survey, about one-third natural size.

Fig. 1. Block of stone showing right half of specimen.
Fig. 2. Left half of skull of same specimen.

PLATE 27.

Gordonia Traquairi.

Cast from same specimen as Plate 26, fig. 2. Left side of skull and lower jaw. Natural size.

PLATE 28.

Gordonia Traquairi.

Casts from same specimen as Plate 26. All the figures natural size.

Fig. 1. Skull seen from above, with right half restored in outline. The median portions are in part drawn from the right half of the specimen.
Fig. 2. View of palate, partly restored.
Fig. 3. Fragment of humerus showing entepicondylar foramen.
Fig. 4. Same specimen, back view.
Fig. 5. Parts of three caudal vertebræ (?).

PLATE 29.

Gordonia Huxleyana, sp. nov.

Specimen belonging to the Geological Survey. Both figures natural size.

Fig. 1. Left half of skull and lower jaw.
Fig. 2. Right half of skull and lower jaw, drawn from the actual specimen, showing the cavities left by the bones and especially the palate.

PLATE 30.

Gordonia Huxleyana.

Same specimen as Plate 29. All figures natural size.

Fig. 1. Skull seen from above, right side restored in outline.
Fig. 2. Left scapula, outer surface.
Fig. 2*a*. „ „ inner surface.
Fig. 3. Clavicle.
Fig. 4. Right humerus wanting both extremities.
Fig. 5. Left ilium.

Gordonia Huxleyana?

The following figures, 6 to 9, are drawn natural size, from casts of a specimen preserved in the Elgin Museum, which is provisionally referred to this species.

Fig. 6. Clavicle.
Fig. 7. Right scapula, outer surface.
Fig. 8. Left humerus, hinder aspect.
Fig. 9. Right humerus, front aspect.

PLATE 31.

Gordonia Duffiana, sp. nov.

From a photograph of two blocks of stone, about one-third natural size, containing a large part of a skeleton, with a skull. Preserved in the Elgin Museum. There is every reason to believe that this skull was found with and belongs to the trunk, but there is no positive proof that such is the case.

PLATE 32.

Gordonia Duffiana.

Same specimen as Plate 31. All the figures natural size.

Fig. 1. Natural cast of the inner parts of the skull. The external surface is shown in fig. 2.
Fig. 2. Upper surface of skull, drawn from a cast of the counterpart of fig. 1. Some of the under parts are seen below this, and the right side and muzzle are completed in outline.
Fig. 3. Occiput.
Fig. 4. Parts of neural arches of three dorsal vertebræ seen from the side.
Fig. 5. Same seen from above.
Fig. 6. Humerus, side view.
Fig. 7. Left ilium, outer surface.

PLATE 33.

Gordonia Duffiana.

Figs. 1 to 4. Same specimen as Plate 31. All figures natural size.

Fig. 1. Skull, side view of natural impression of inner parts; same specimen as Plate 31, fig. 1.
Fig. 2. Same specimen, right orbit.
Fig. 3. Same as fig. 1, with cast of upper surface in its natural position, and outline of muzzle restored.
Fig. 4. Restored view of palate. Drawn partly from casts and partly from measurements.

Gordonia?

Fig. 5. Caudal vertebræ with transverse processes, provisionally referred to *Gordonia.* Preserved in the Elgin Museum.

PLATE 34.

Gordonia Traquairi?

From a photograph of a block of sandstone containing a nearly entire skeleton provisionally referred to this species. About half natural size. Preserved in the Elgin Museum.

PLATE 35.

Gordonia Traquairi?

Figs. 1 to 5. Same specimen as Plate 34. All figures natural size.

Fig. 1. Skull seen from above, right side partly restored in outline.
Fig. 2. Same, side view of skull and lower jaw. The post-orbital bar and tip of muzzle partly restored.
Fig. 3. Left scapula, outer surface.
Fig. 4. Left humerus, oblique view of hinder and outer surfaces.
Fig. 4*a*. Same, from outer side.
Fig. 4*b*. Same, outline of distal extremity.
Fig. 5. Left radius and ulna.

Gordonia Juddiana, sp. nov.

Figs. 6 to 8. All the figures natural size. Preserved in the Elgin Museum.

Fig. 6. Skull seen from above, right temporal arcade restored in outline.
Fig. 7. Same specimen, left side.
Fig. 8. Same specimen, occiput with part of right side restored.

PLATE 36.

Geikia Elginensis, gen. et sp. nov.

All the figures natural size. Specimen preserved in the Elgin Museum.

Fig. 1. Skull seen from above.
Fig. 2. Same, right side.
Fig. 3. Same, front view.
Fig. 4. Same, occiput.
Fig. 5. Lower jaw, left ramus.

PLATE 37.

Elginia mirabilis, gen. et sp. nov.

In the possession of the Geological Survey.

Fig. 1. Skull seen from right side. Natural size. The upper part of the temporal region has been drawn from the opposite side (see Plate 38), and the teeth

have been restored in outline. The positions of some of the sutures are indicated by fine lines.

Fig. 2. Portion of left maxilla and premaxilla with teeth *in situ.* Natural size.

Fig. 3. Outer view of tooth enlarged two diameters.

Fig. 4. Tooth from inner side enlarged two diameters.

PLATE 38.

Elginia mirabilis.

Same specimen as Plate 37, natural size. Skull seen directly from above. The portion represented without ornament is wanting in the original, and has been restored from the opposite side.

PLATE 39.

Elginia mirabilis.

Same specimen as Plates 37 and 38, seen from below. Natural size. Showing palate and base of skull.

PLATE 40.

Elginia mirabilis.

Same specimens as Plates 37 to 39, seen from behind and partly from below. Natural size.

PLATE 41.

Sacrum and Vertebræ.

Both the specimens figured on this Plate are from the Elgin Sandstone, but it is not quite certain that they are from Cuttie's Hillock Quarry. Their affinities are uncertain. They are represented natural size.

Fig. 1. Two late dorsal or lumbar vertebræ belonging to the Geological Survey, seen from the left side with the neural spines restored in outline. These two vertebræ are said to have been found with the skull of *Elginia.*

Fig. 2. Posterior end of the hindermost vertebra of fig. 1.

Fig. 3. Diagrammatic section through the two vertebral centra to show the thin bone which covered the notochord.

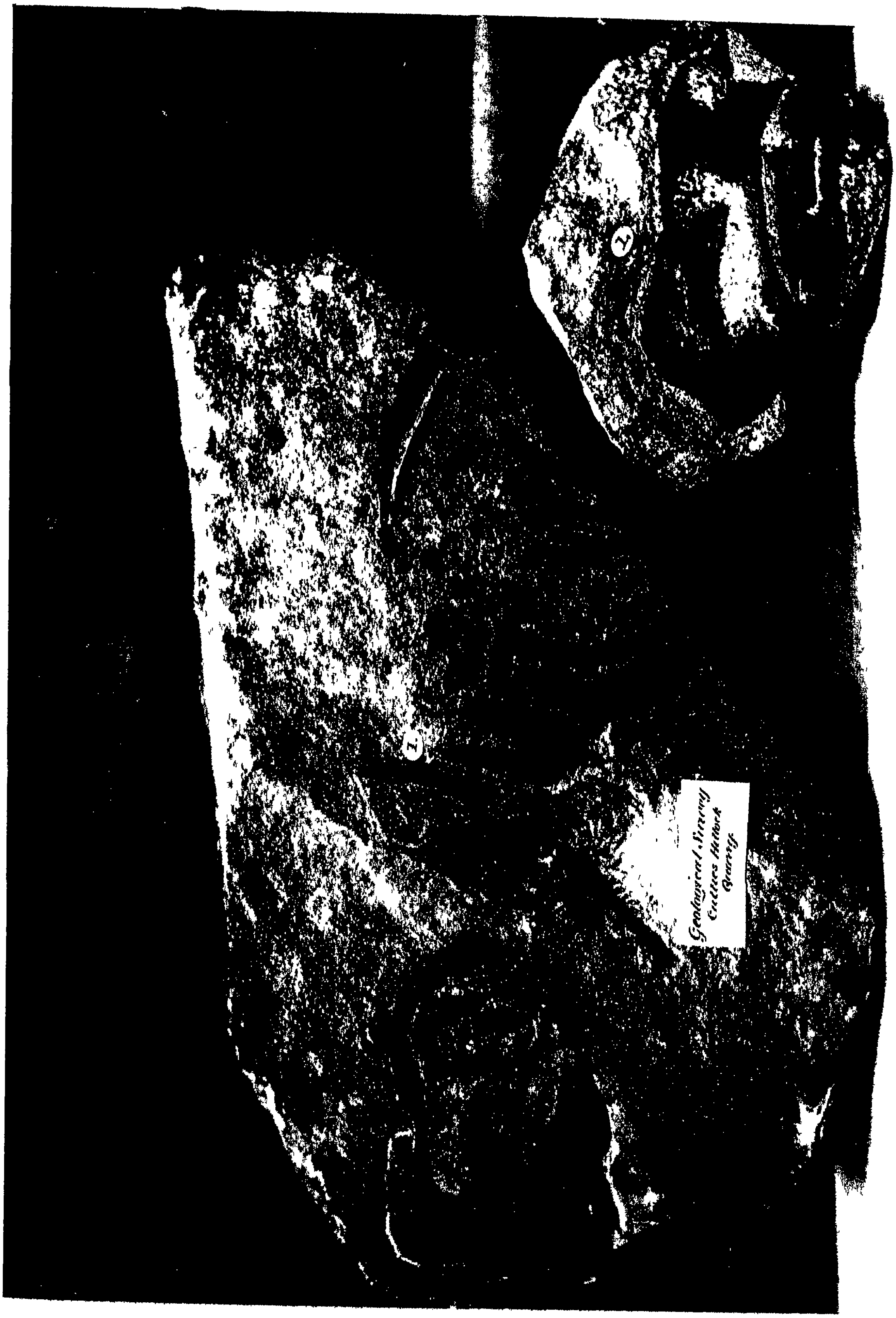
Fig. 4. Sacrum, with two presacral vertebræ, seen from below, and showing the large sacral rib. The three hinder vertebræ (to the left of the Plate) show

little more than half of each centrum, the left side having been crushed. The left sides of the other vertebræ are also imperfect. Preserved in the Elgin Museum.

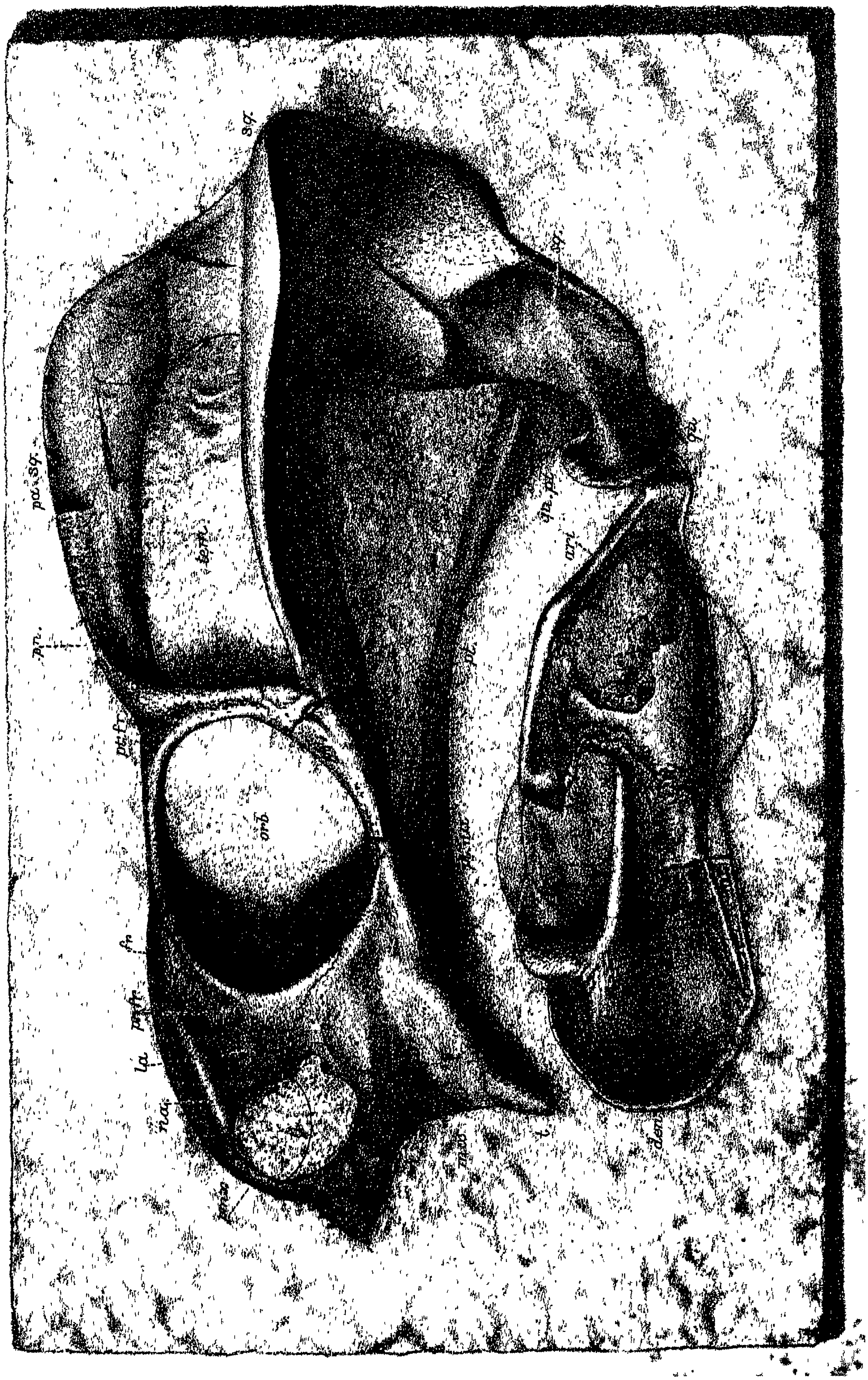
Fig. 5. Same specimen seen from right side.

LETTERING USED IN FIGURES.

art.	Articular bone of lower jaw.
den.	Dentary „ „
eo.	Exocciptal.
ep.o.	Epiotic.
eth.vo.	Ethmo-vomerine septum.
fm.	Foramen magnum.
fr.	Frontal.
i.pa.	Interparietal.
i.pt.	Infra post-temporal fossa.
ju.	Jugal.
la.	Lachrymal.
mx.	Maxilla.
n.	External nasal aperture.
na.	Nasal bone.
orb.	Orbit.
o.sp.	Orbito-sphenoid.
pa.	Parietal.
pa.sq.	Parieto-squamosal crest.
p.fr.	Prefrontal.
pl.	Palatine.
p.mx.	Premaxilla.
pn.	Pineal fossa.
pt.	Pterygoid.
pt.f.	Pterygoid foramen.
pt.fr.	Postfrontal.
pt.o.	Postorbital.
pt.na.	Posterior nares.
qu.	Quadrate.
qu.pt.	Quadrate process of pterygoid.
s.pt.	Supra post-temporal fossa.
sq.	Squamosal.
st.	Supratemporal.
t.	Tusk.
tem.	Temporal fossa.

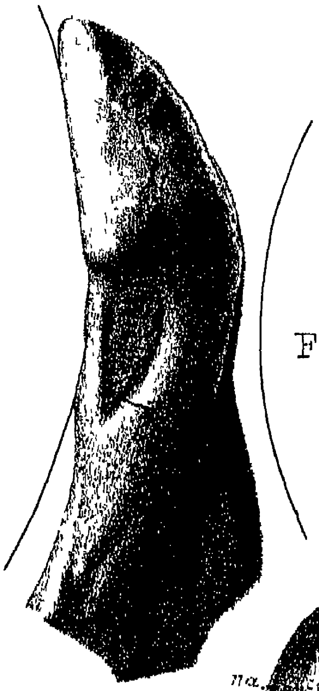


GORDONIA TRAQUAIRI, *gen. et sp. nov.*



Gordonia Traquari. *sp.nov.*

A T Hollick, lith.



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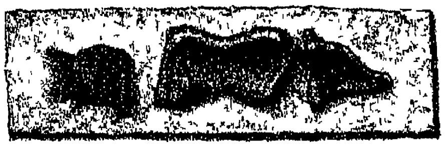

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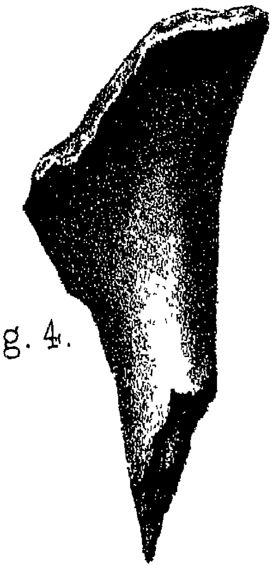


Fig. 4.

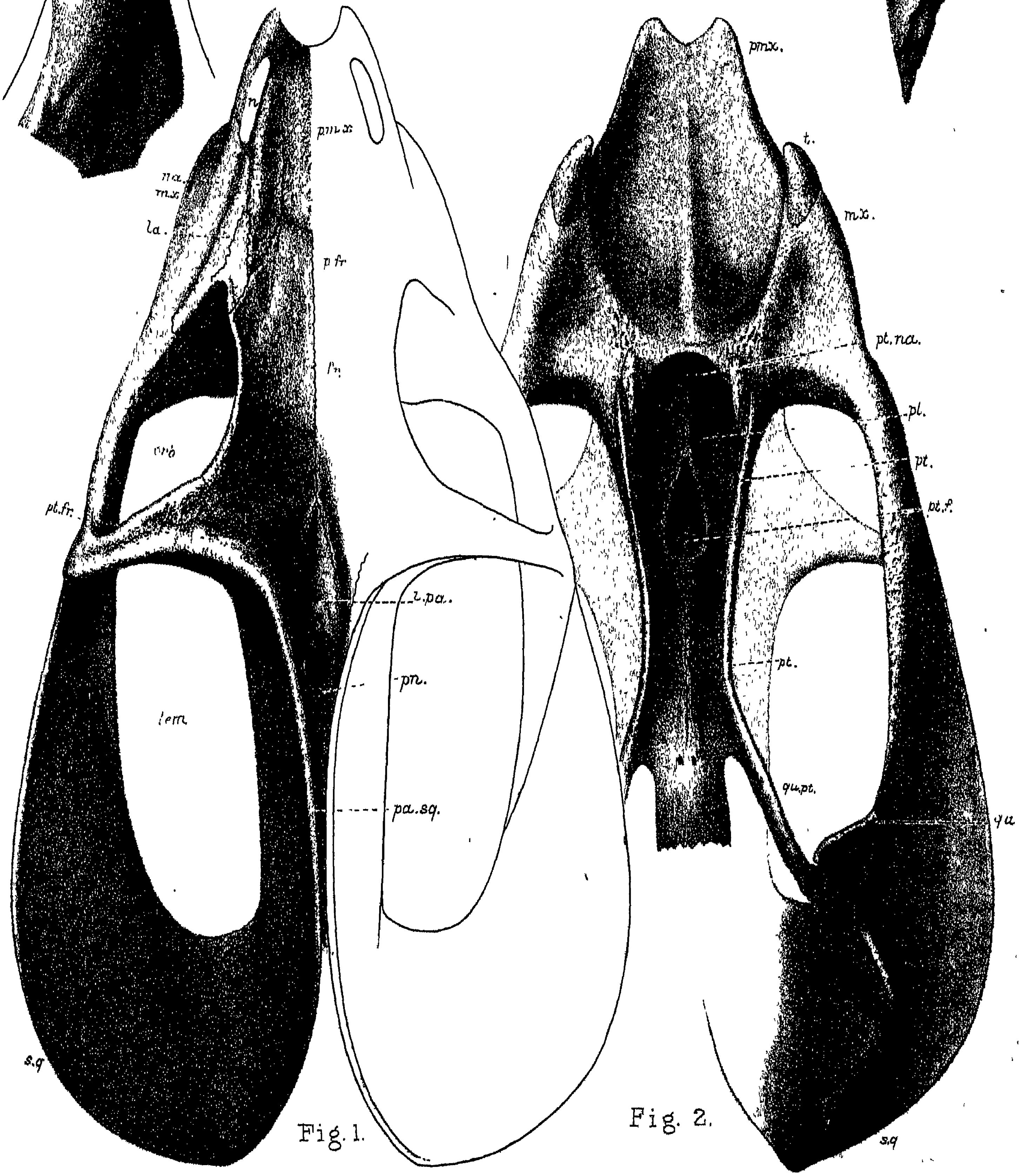


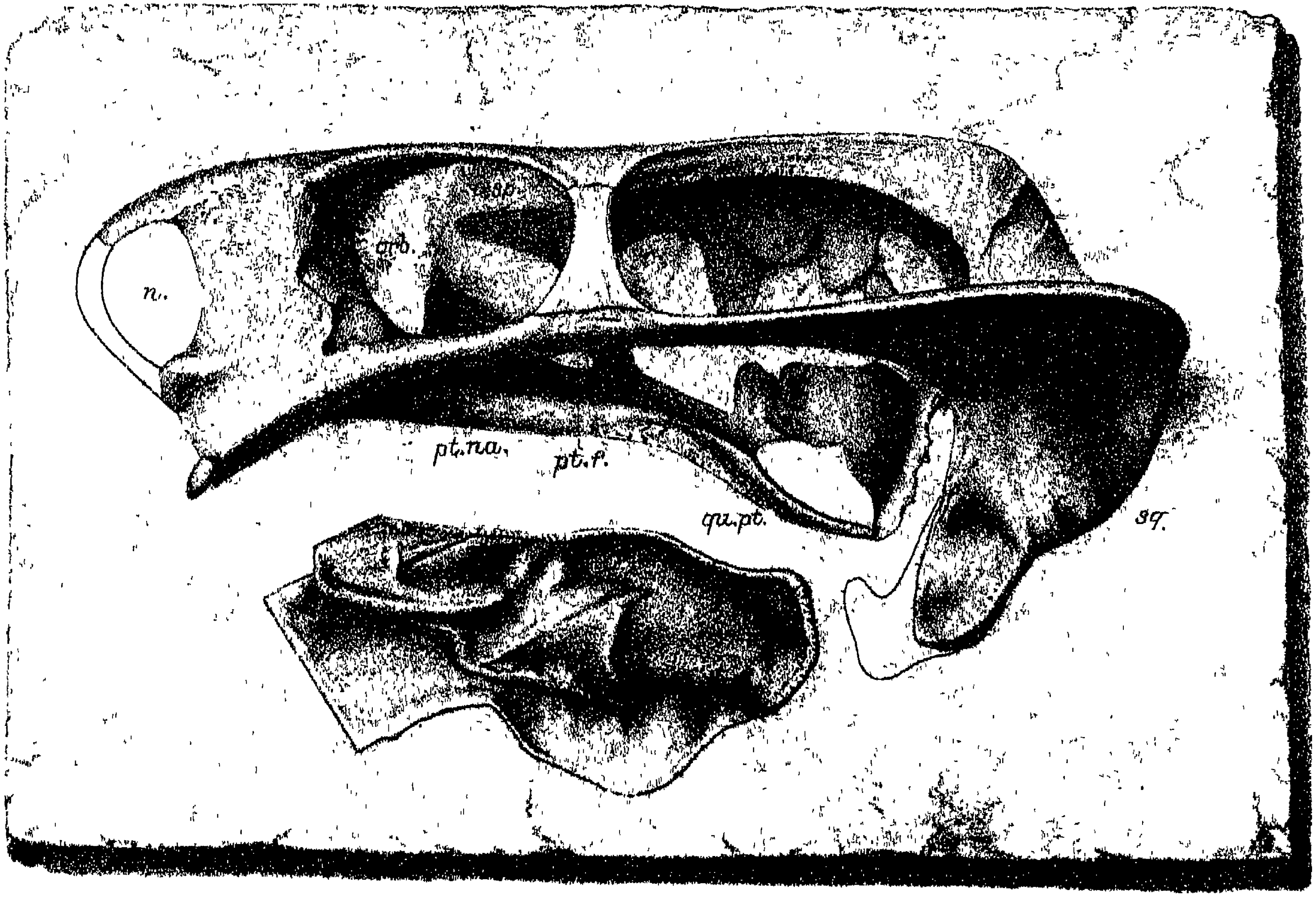
Fig. 1. Fig. 2.

A.T. Hollick. lith.

Gordonia Traquairi, *sp. nov.*

West, Newman.

Fig. 1.



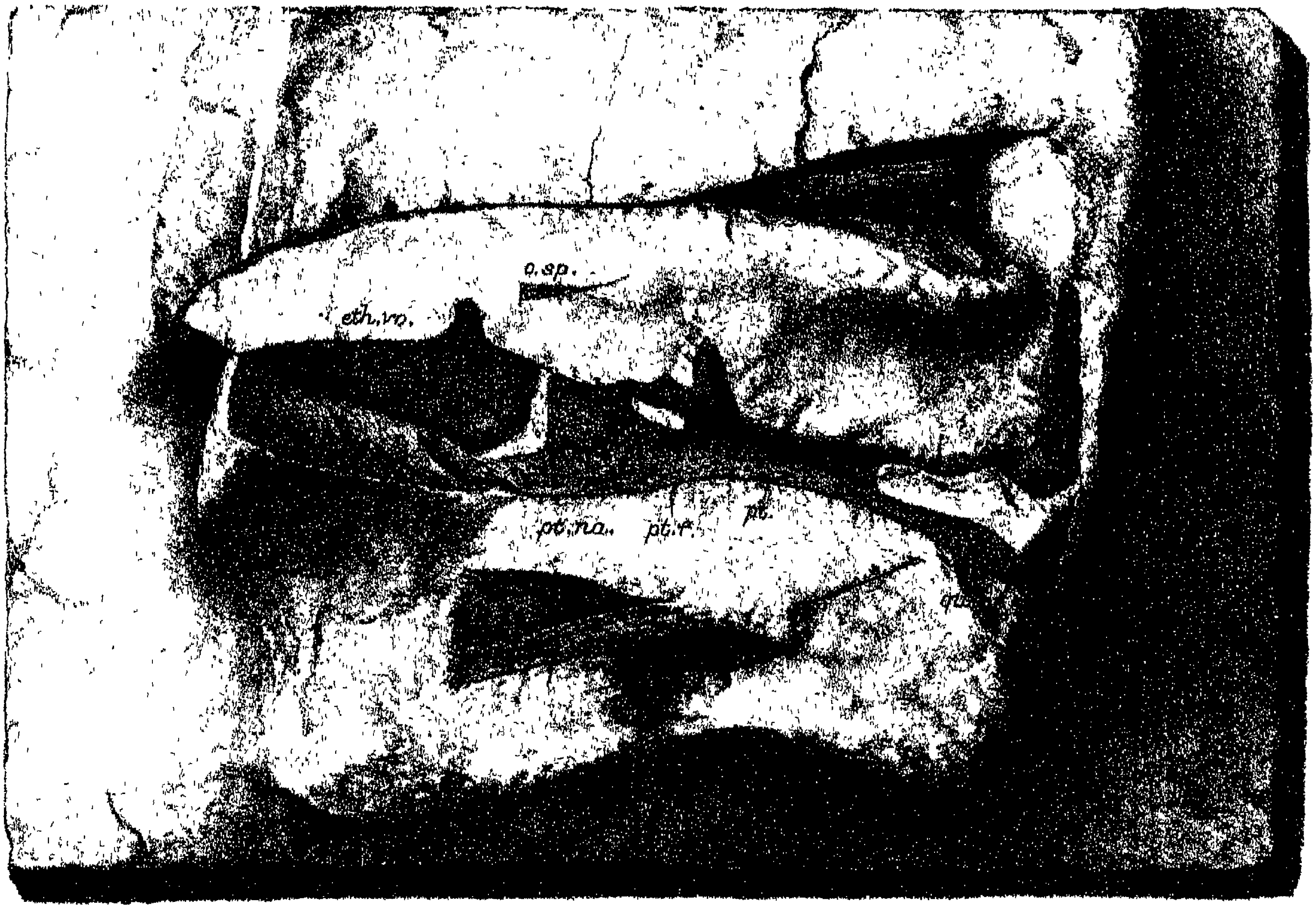


Fig. 2.

A. T. Hollick lith. West, Newman imp.

Gordonia Huxleyana, *sp. nov.*

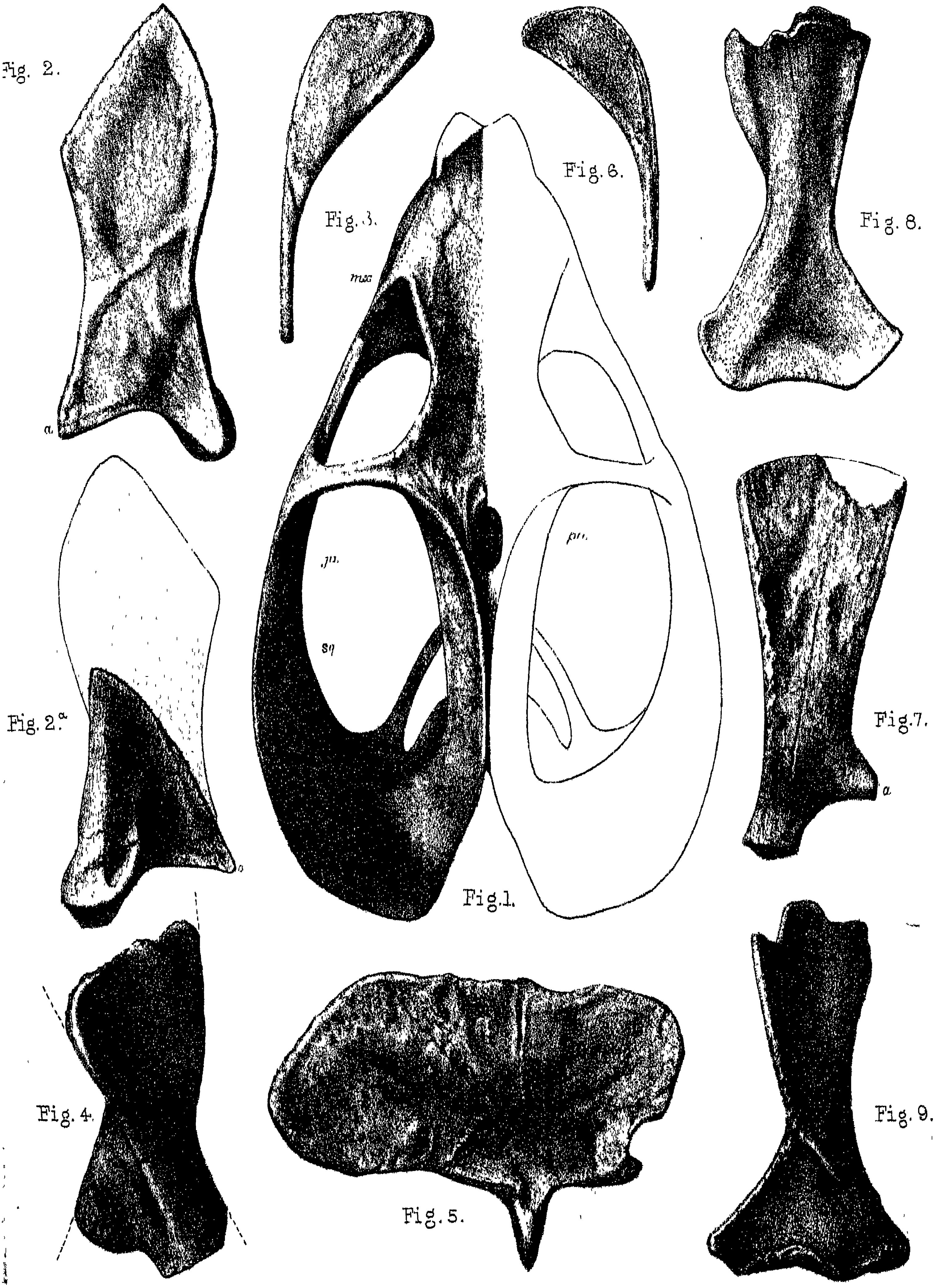
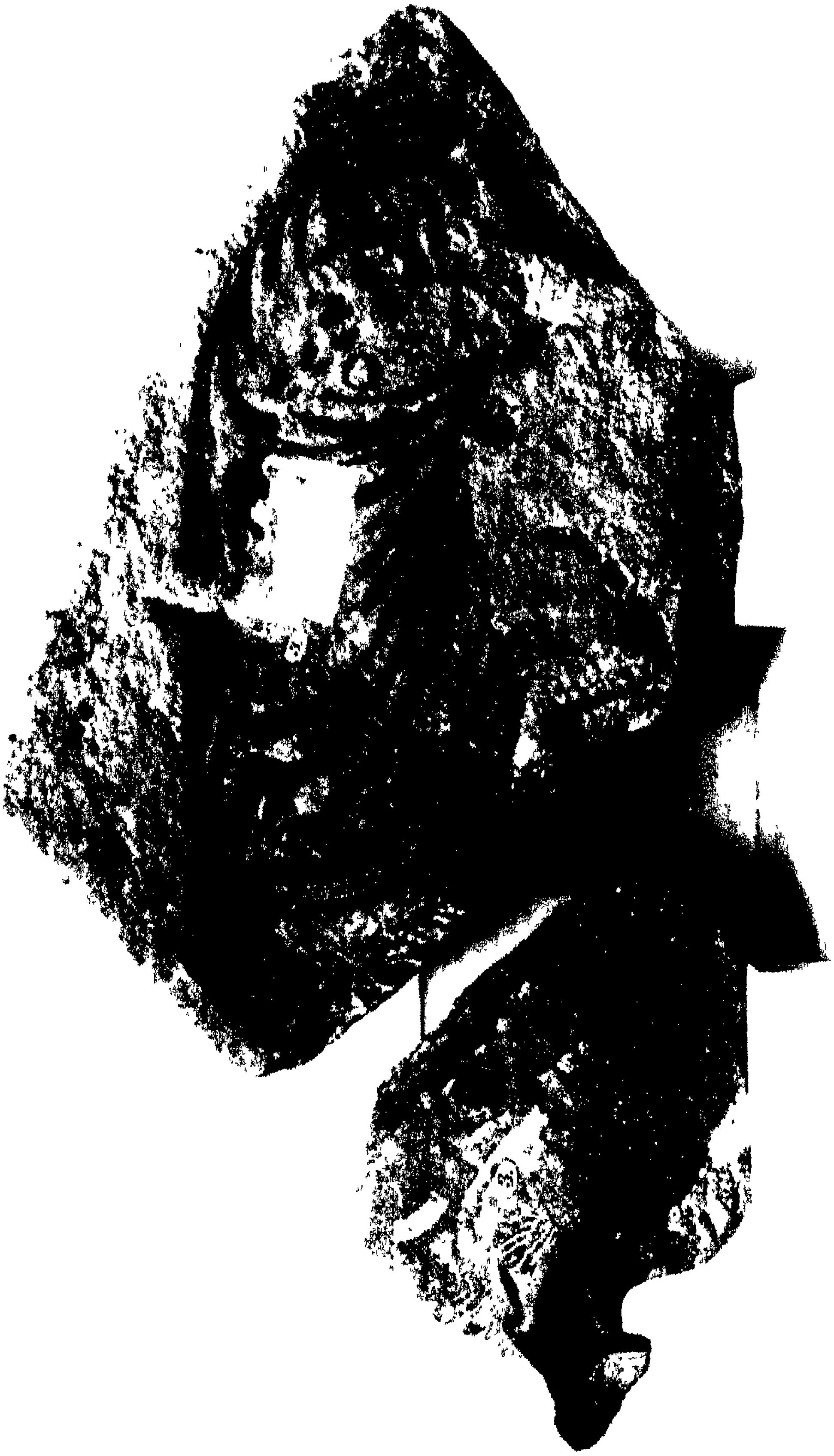


Fig. 2.
a
Fig. 3.
mx
Fig. 6.
Fig. 8.
jn
sq
pn
Fig. 2.a
a
Fig. 7.
a
Fig. 1.
Fig. 4.
Fig. 5.
Fig. 9.

A.T.Hollick lith

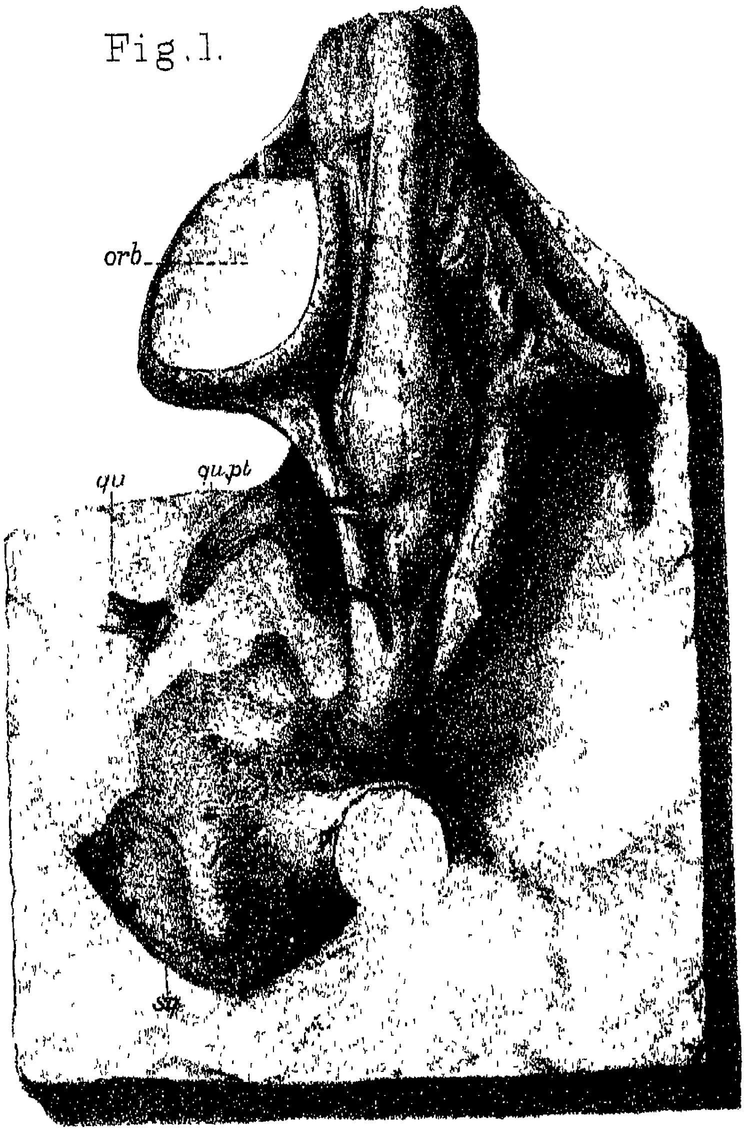
West,Newman imp.

Gordonia Huxleyana, *sp. nov.*



GORDONIA DUFFIANA, sp. nov.

Fig. 1.



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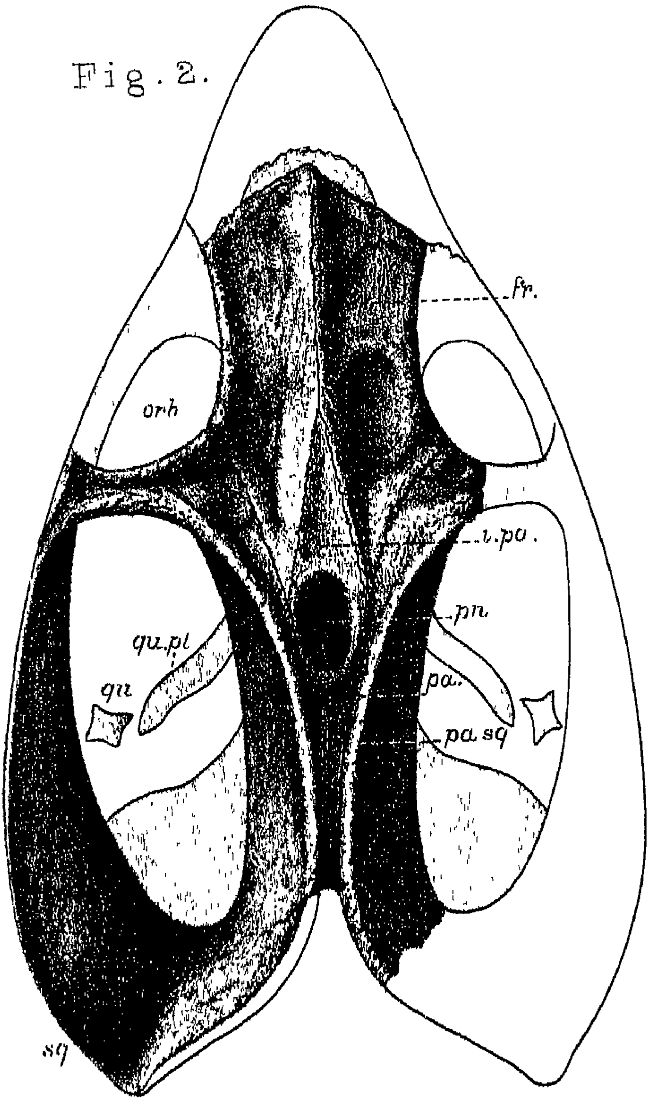

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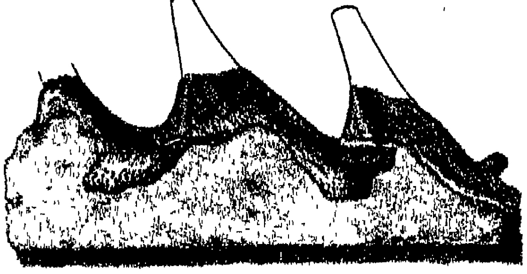


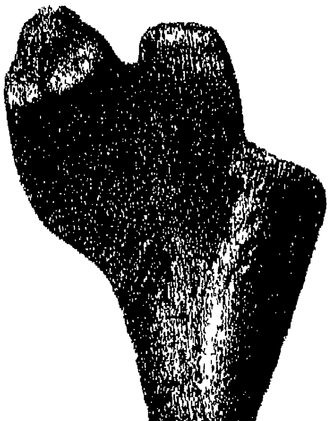
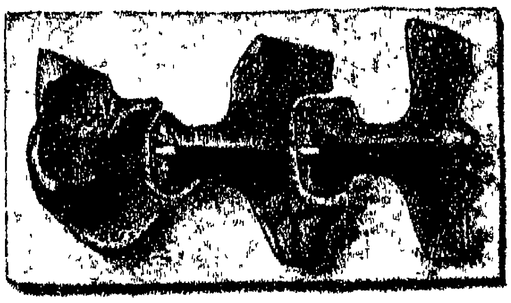
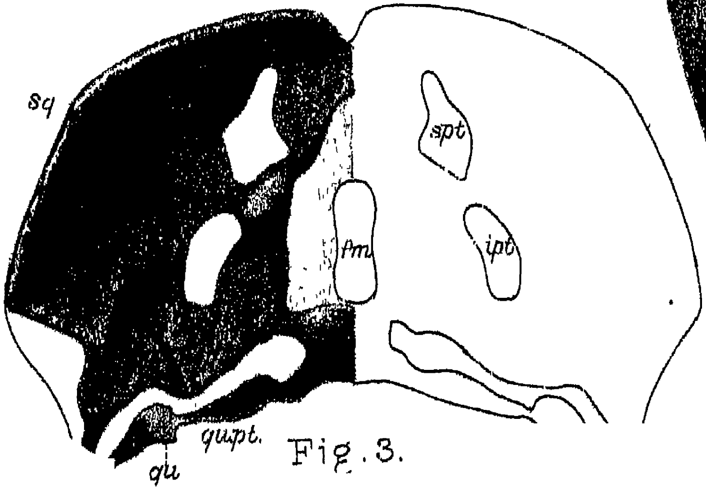


Fig. 6.

Fig. 5.





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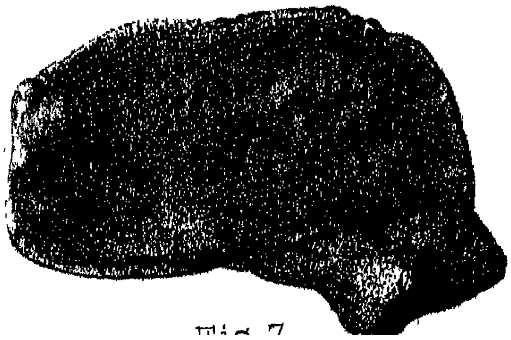


Fig. 7.

A.T. Hollick, lith.

West, Newman imp.

Gordonia Duffiana, *sp. nov.*

Fig. 2.

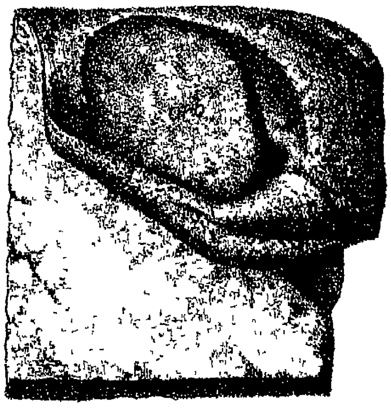
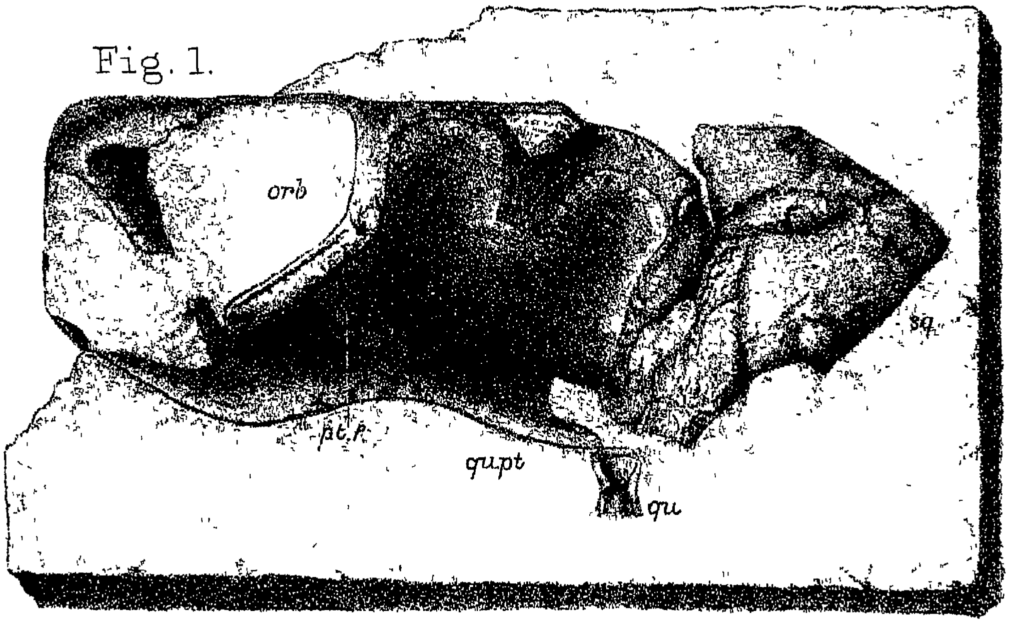


Fig. 1.



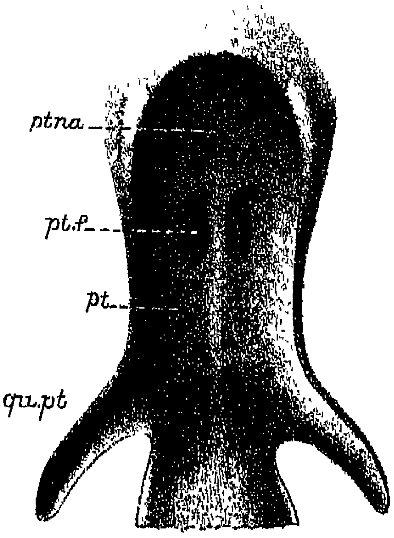
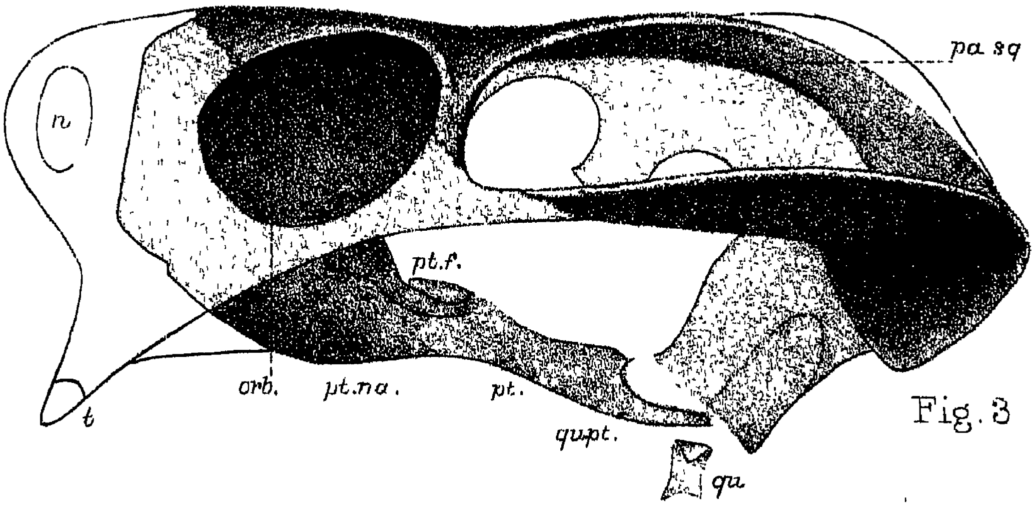


Fig. 4



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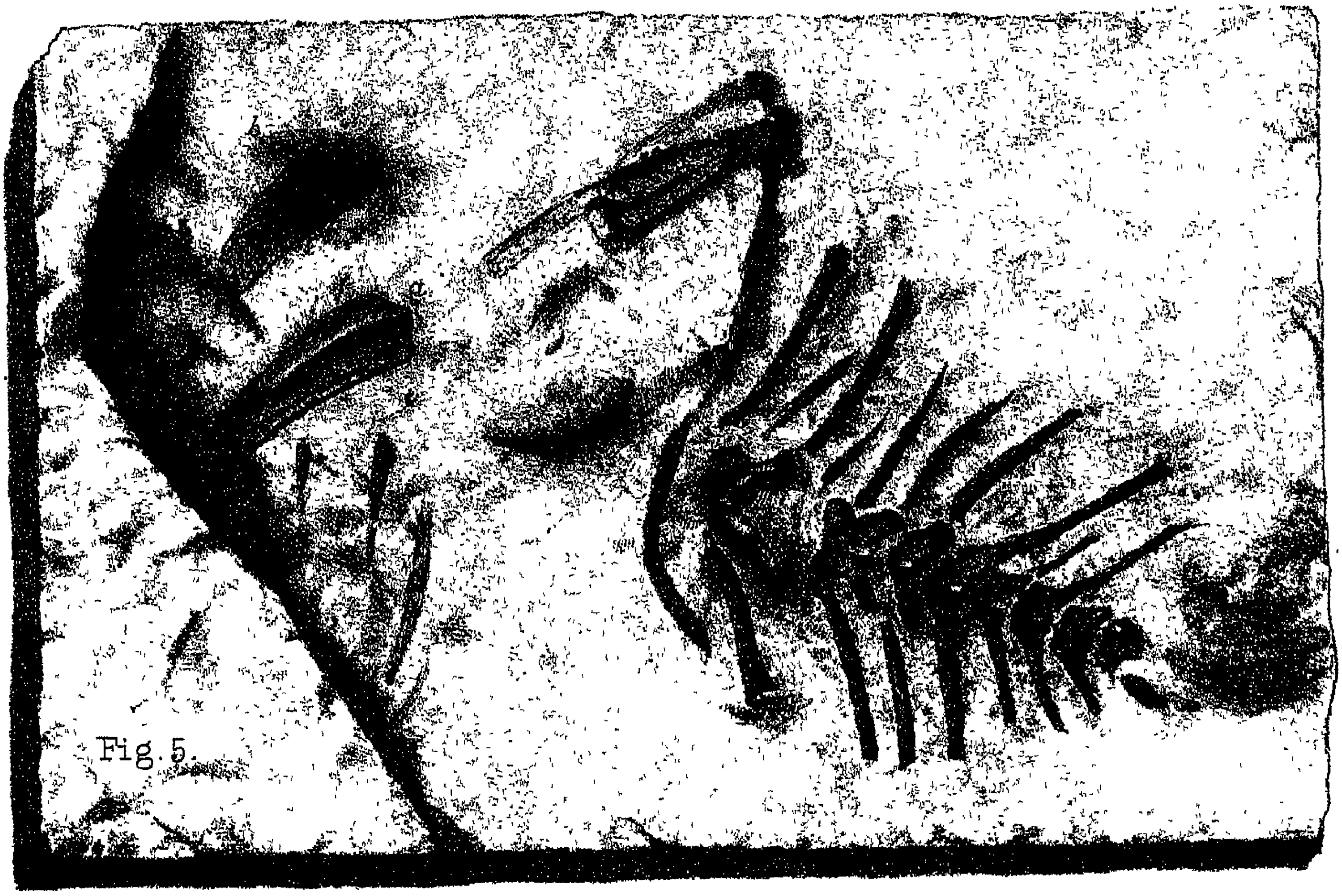
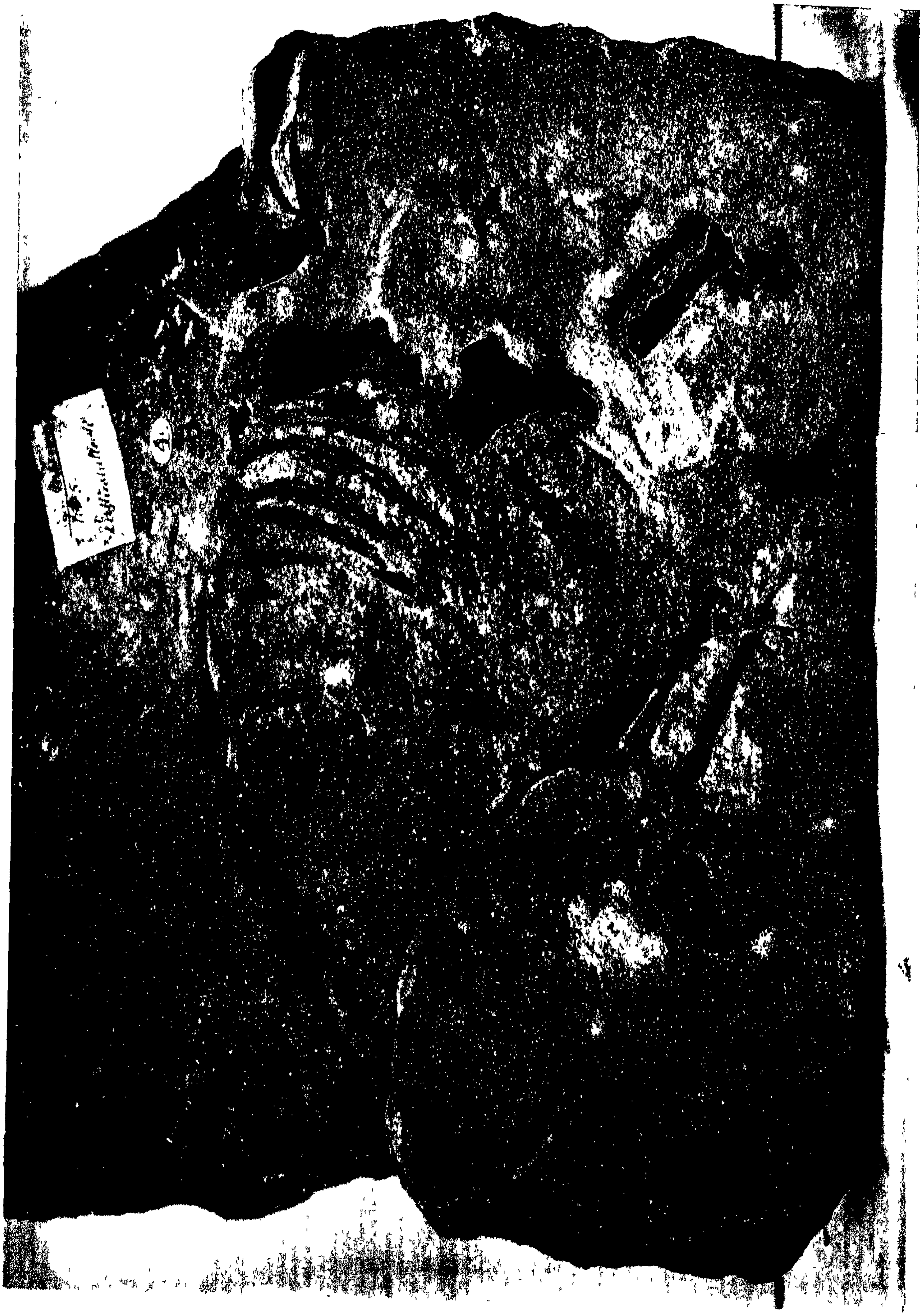


Fig. 5.

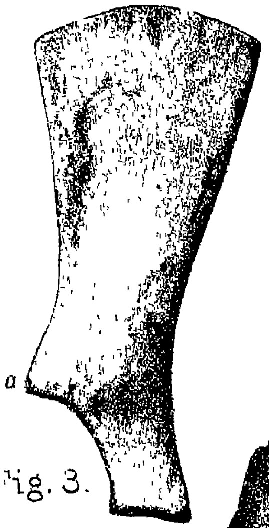
A.T. Hollick, lith.

West, Newman imp.

1-4 Gordonia Duffiana *sp. nov.*
5 Gordonia ?



GORDONIA TRAQUAIRI, sp. nov.



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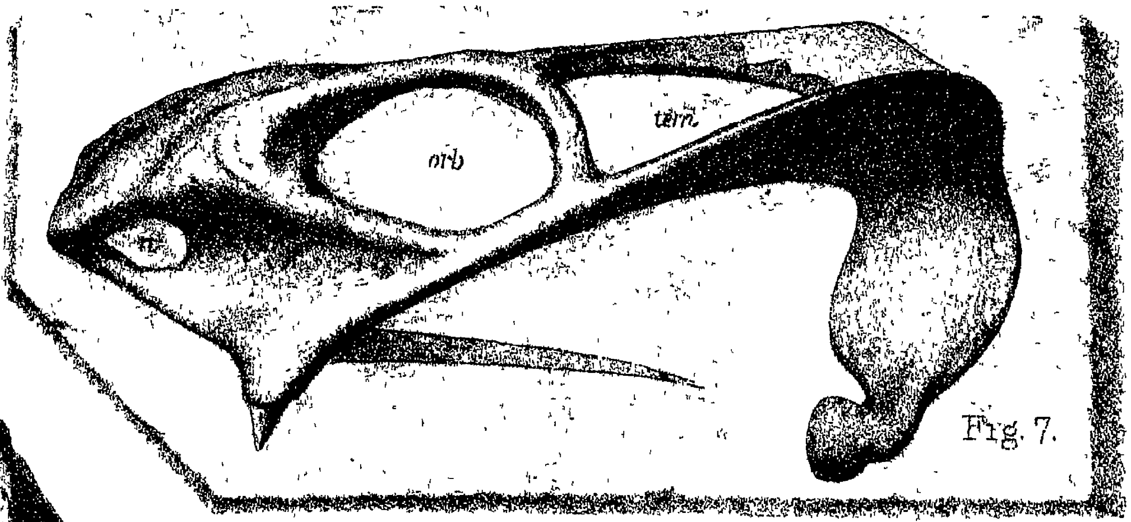
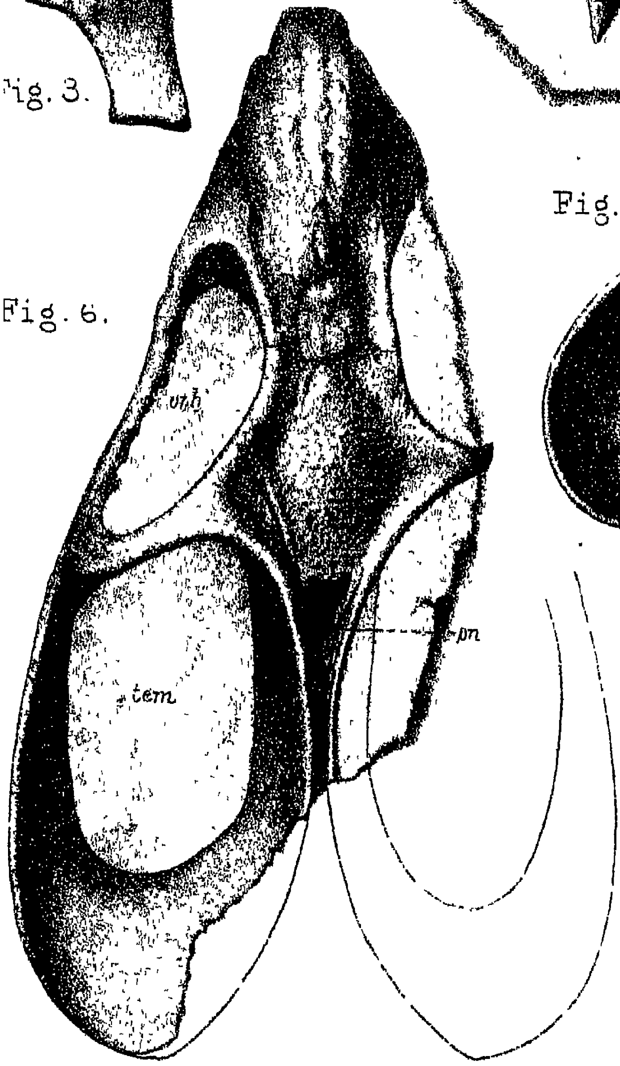


Fig. 7.



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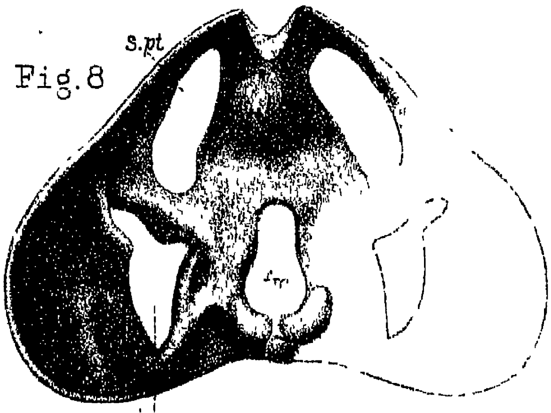


Fig. 8

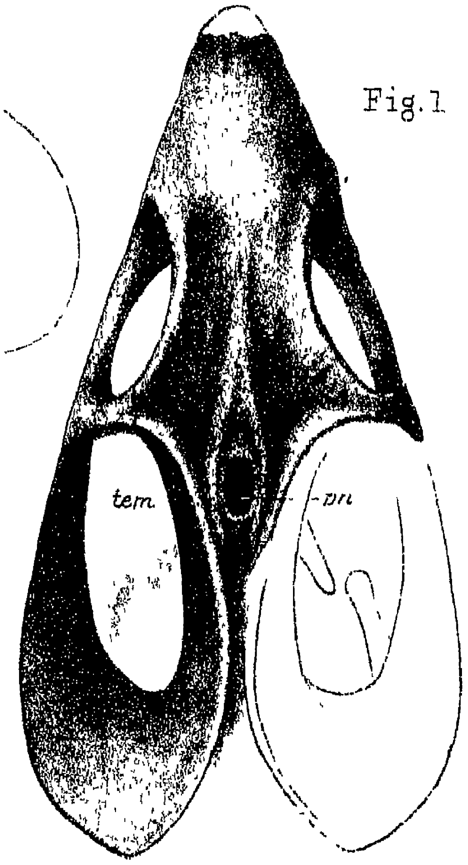


Fig. 1

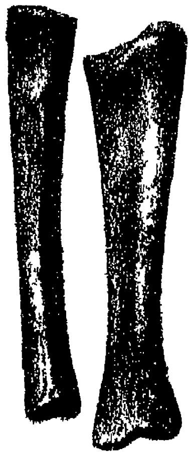


Fig. 5.

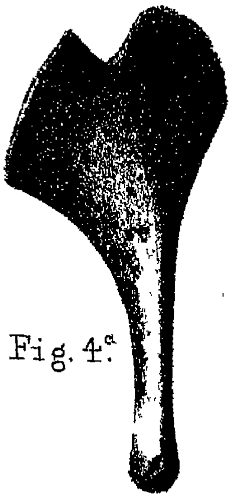


Fig. 4a.

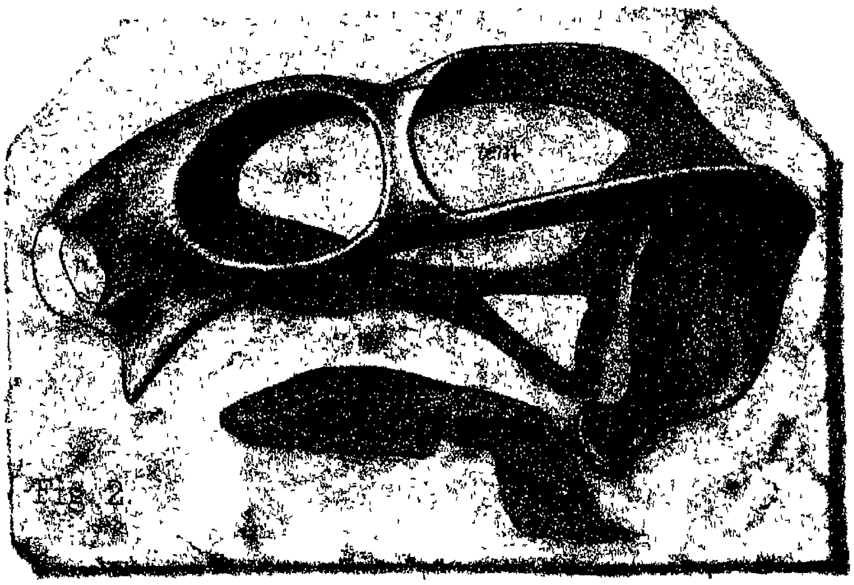


Fig. 2.

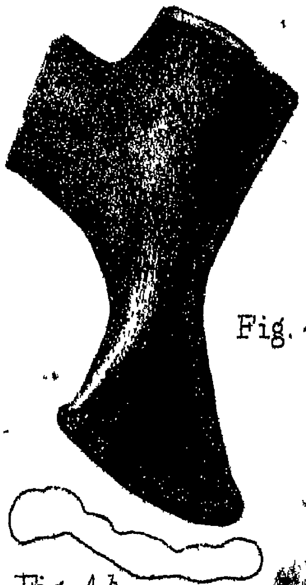
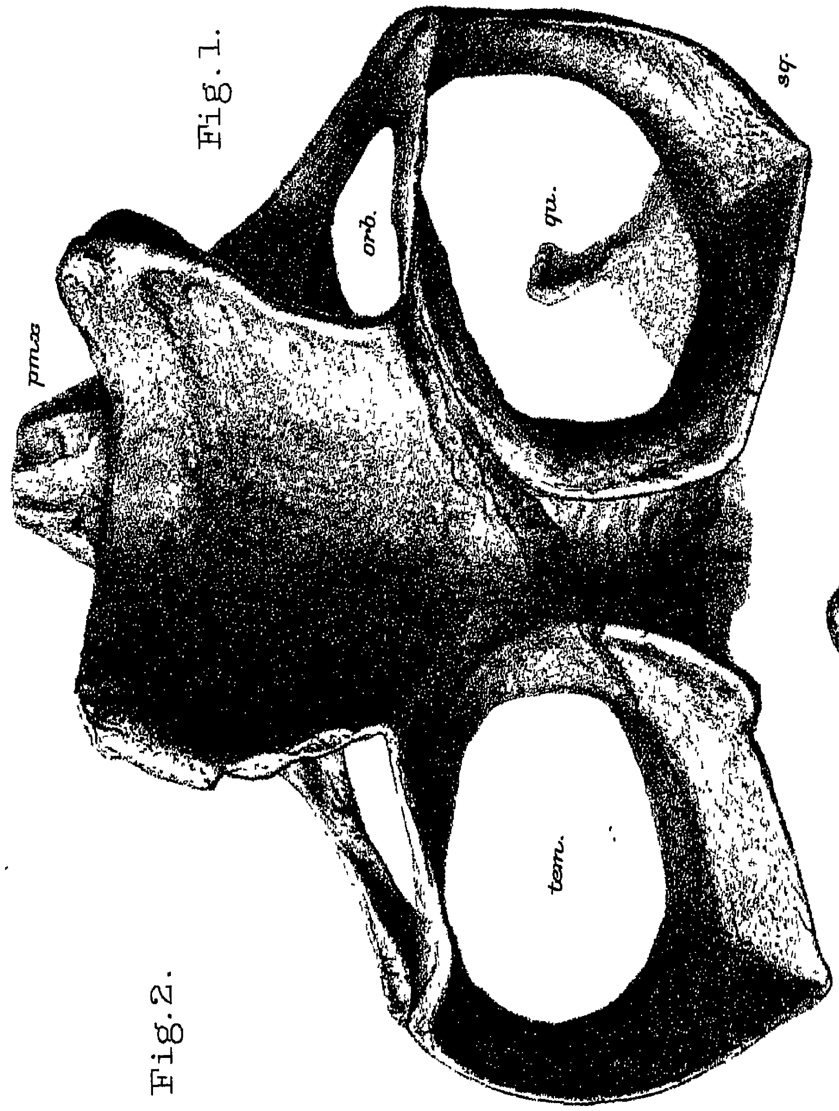


Fig. 4

Fig. 4b.

A. T. Hollick lith. West, Newman imp.

1-5 Gordonia Traquairi, ? *sp. nov.*
6-8 Gordonia Juddiana *sp. nov.*



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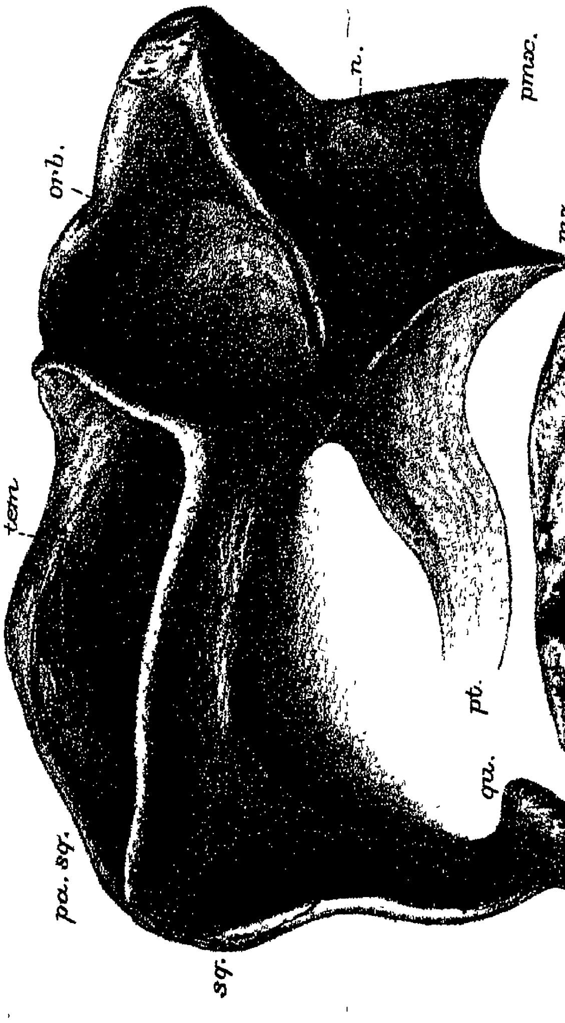

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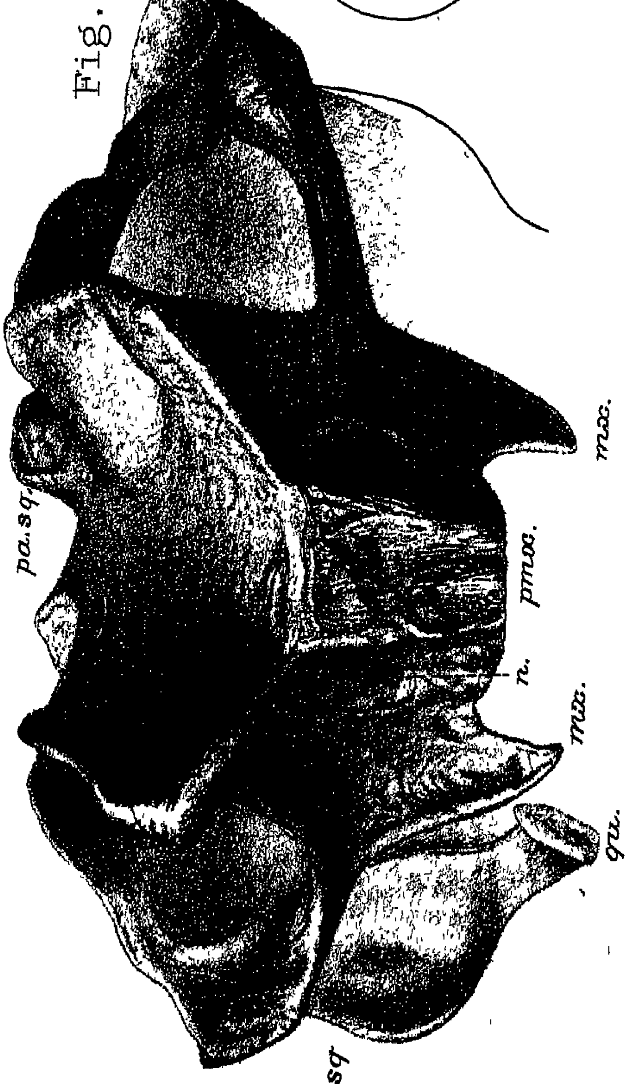


Fig. 3.

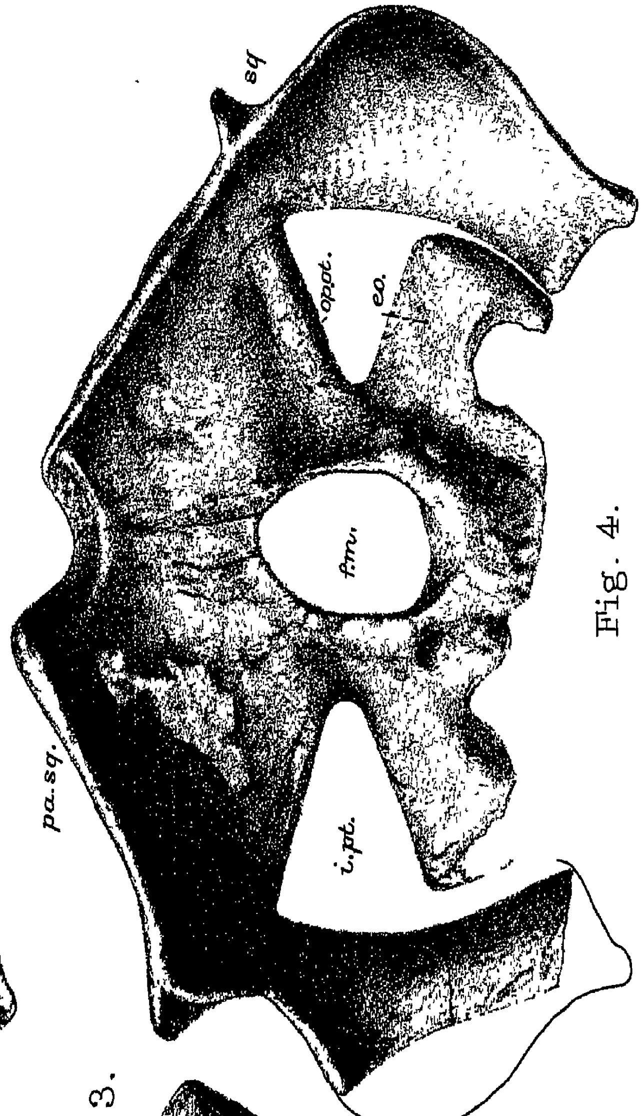


Fig. 4.

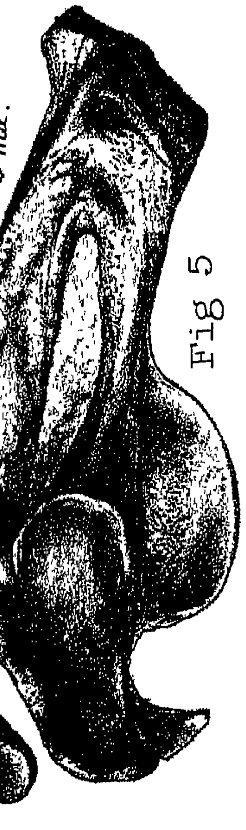


Fig 5

Geikia Elginensis gen. et. sp. nov.

A.T. Hollick lith.
West, Newman imp.

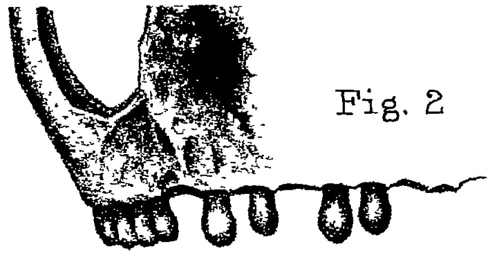


Fig. 2

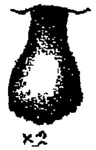


Fig 3.

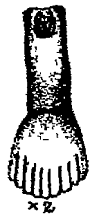
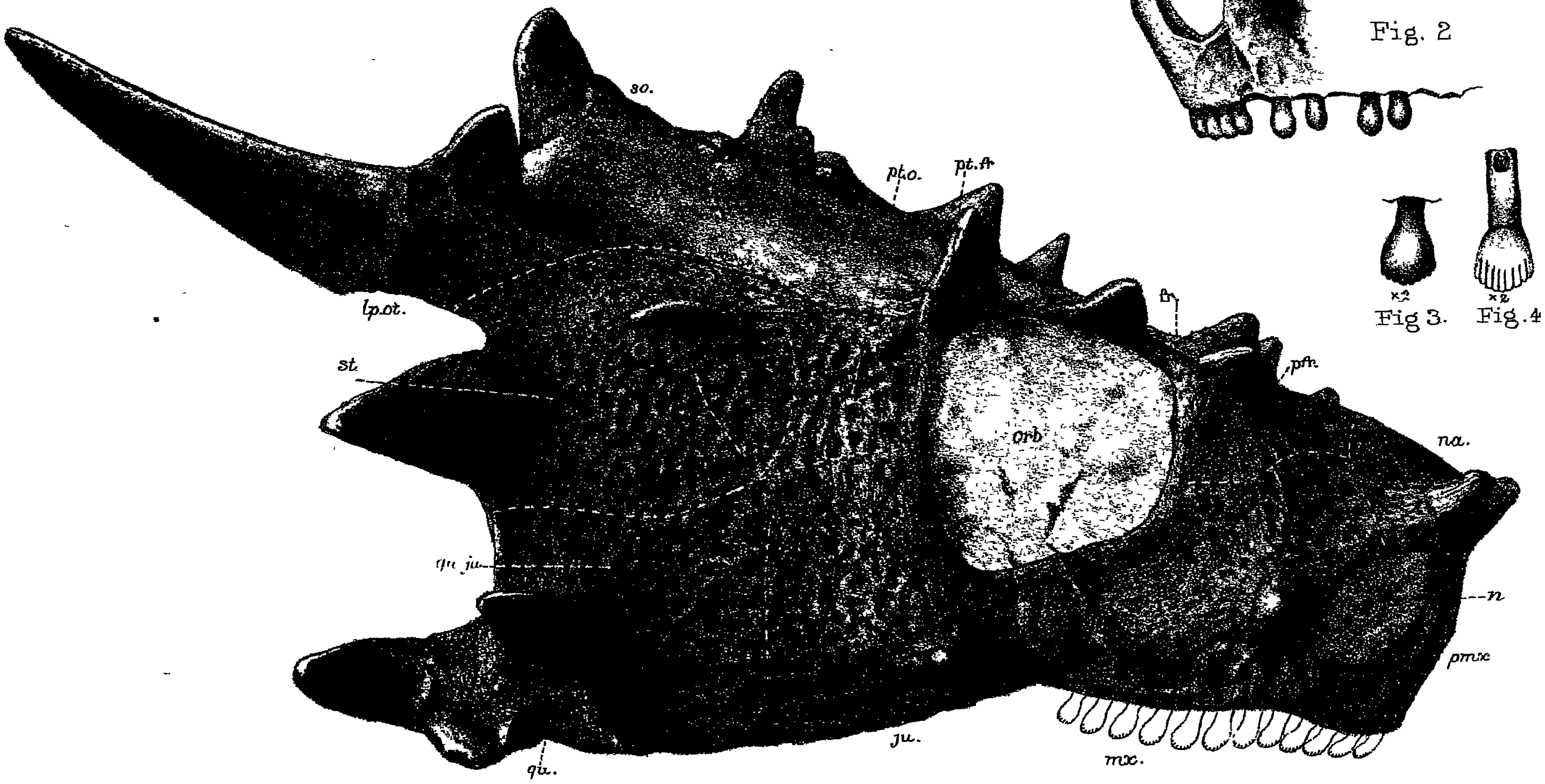


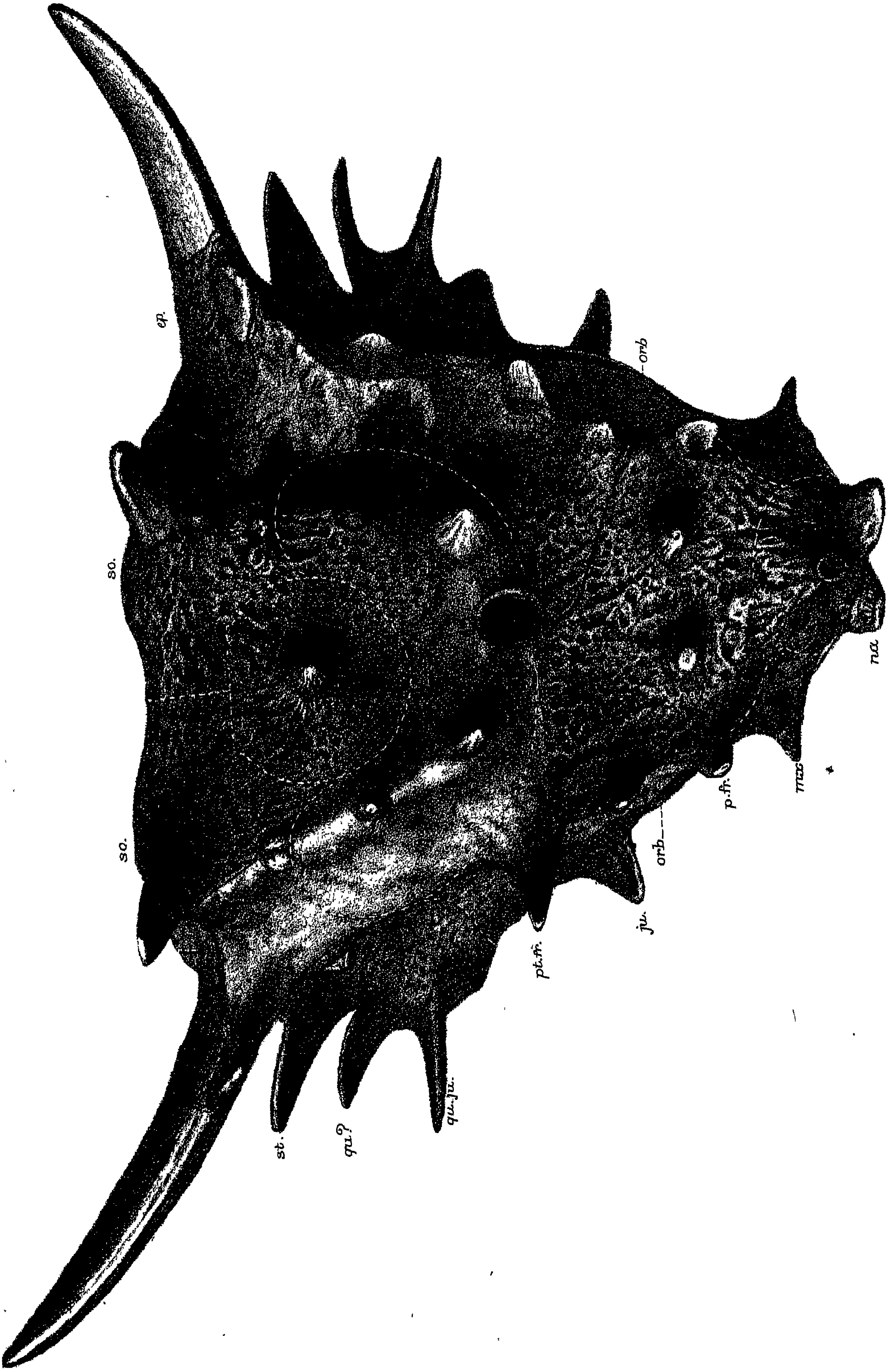
Fig. 4



Fig

Elginia mirabilis, *gen. et sp. nov.*

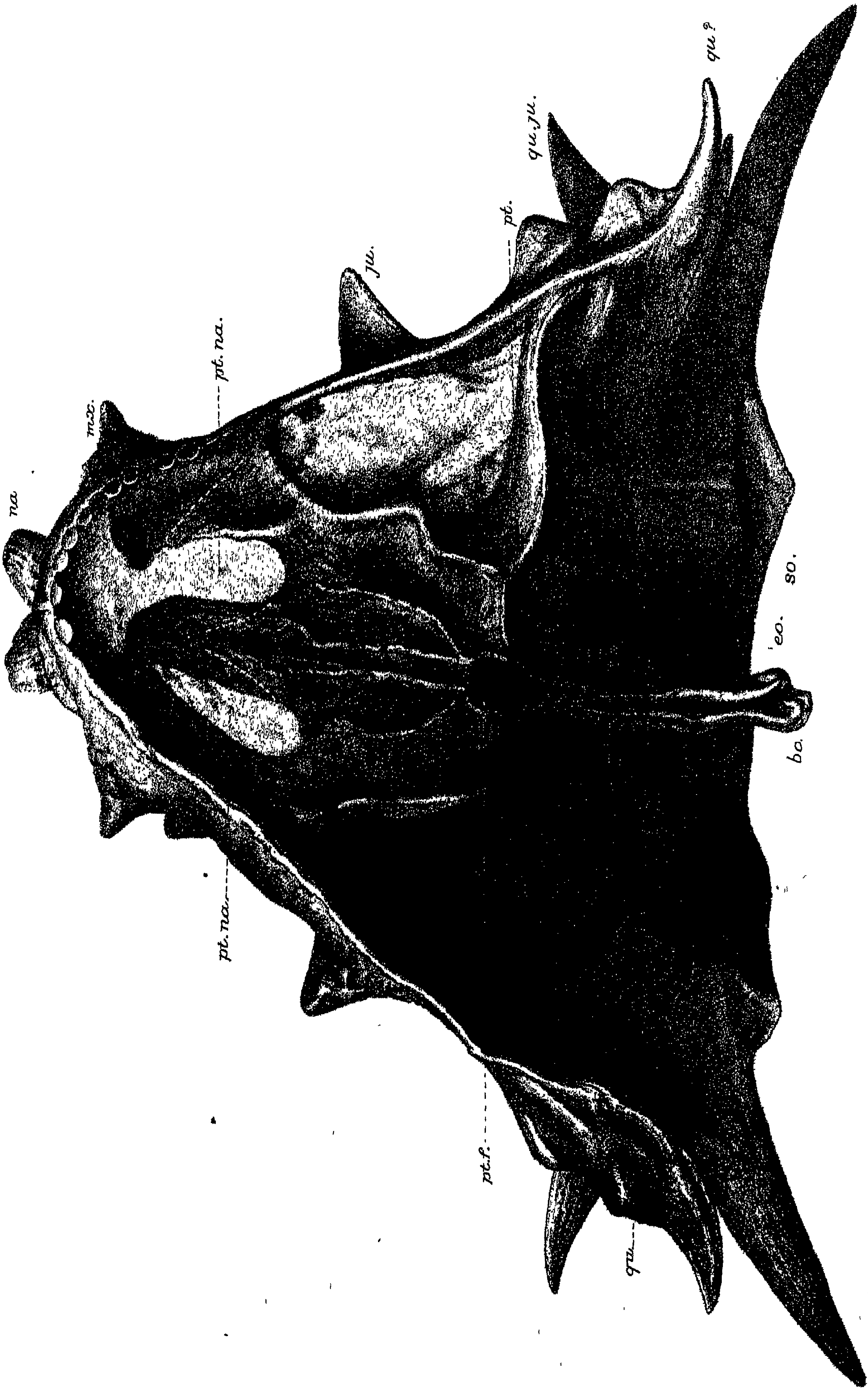
West, Newman imp.



Elginia mirabilis. *gen. et sp. nov.*

[illegible] Hollick lith.

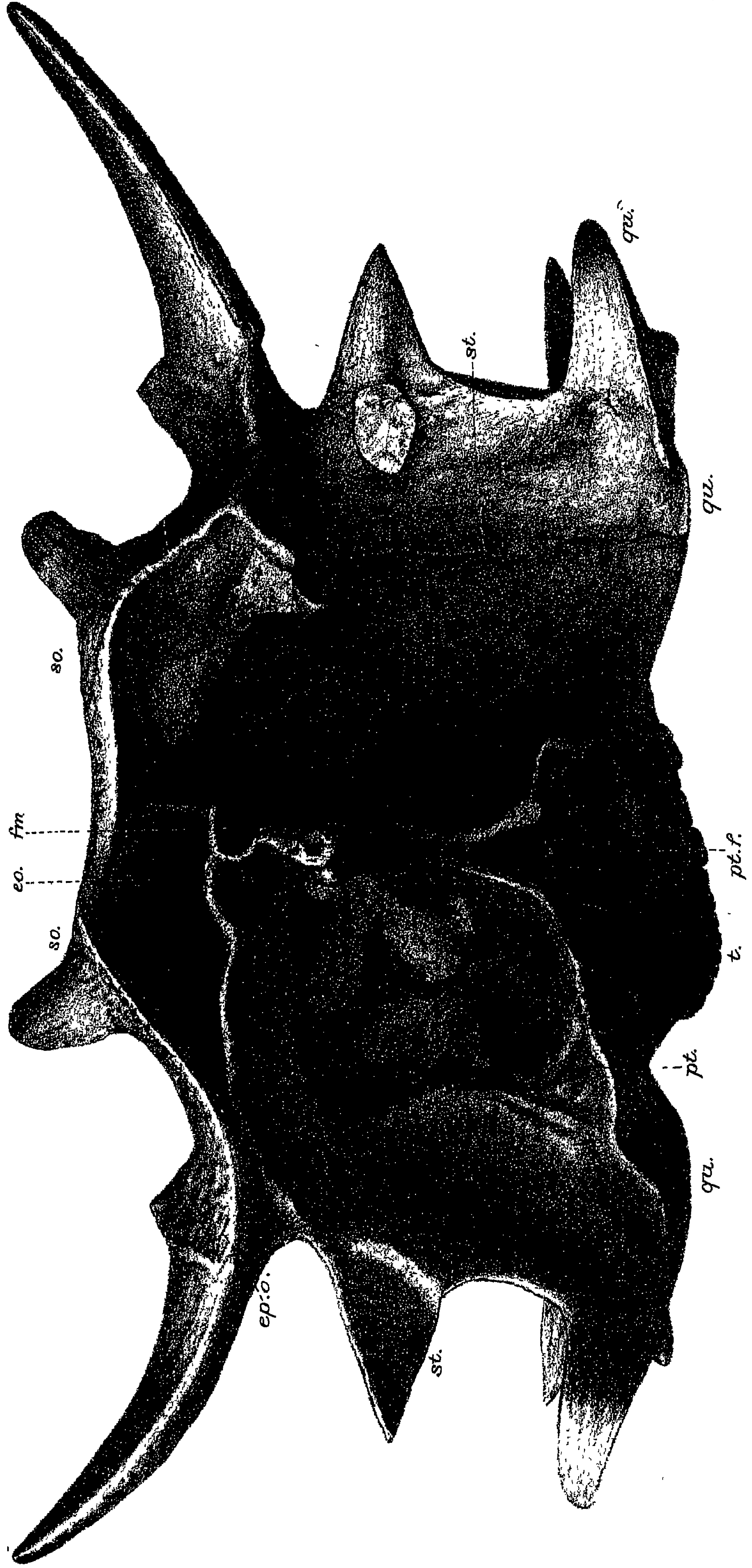
West, Newman imp.



Elginia mirabilis, *gen. et sp. nov.*

F. Holhck lith.

West, Newman imp.



Elginia mirabilis, *gen. et sp. nov.*

A.T. Hollick lith.

West, Newman imp.

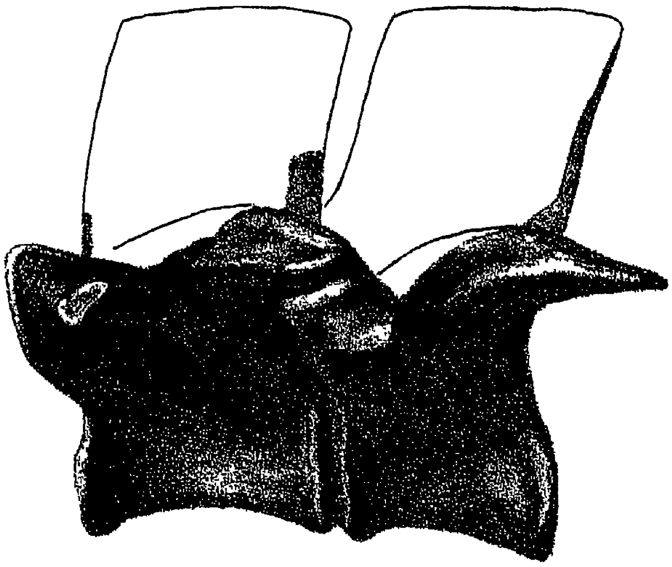


Fig. 1.

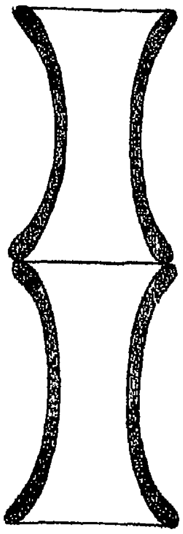


Fig. 3.

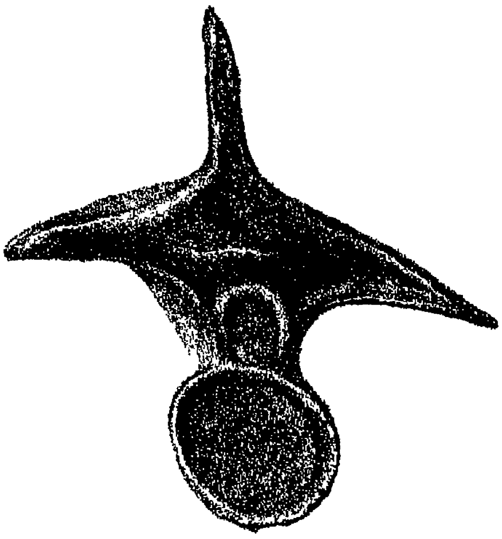


Fig. 2.

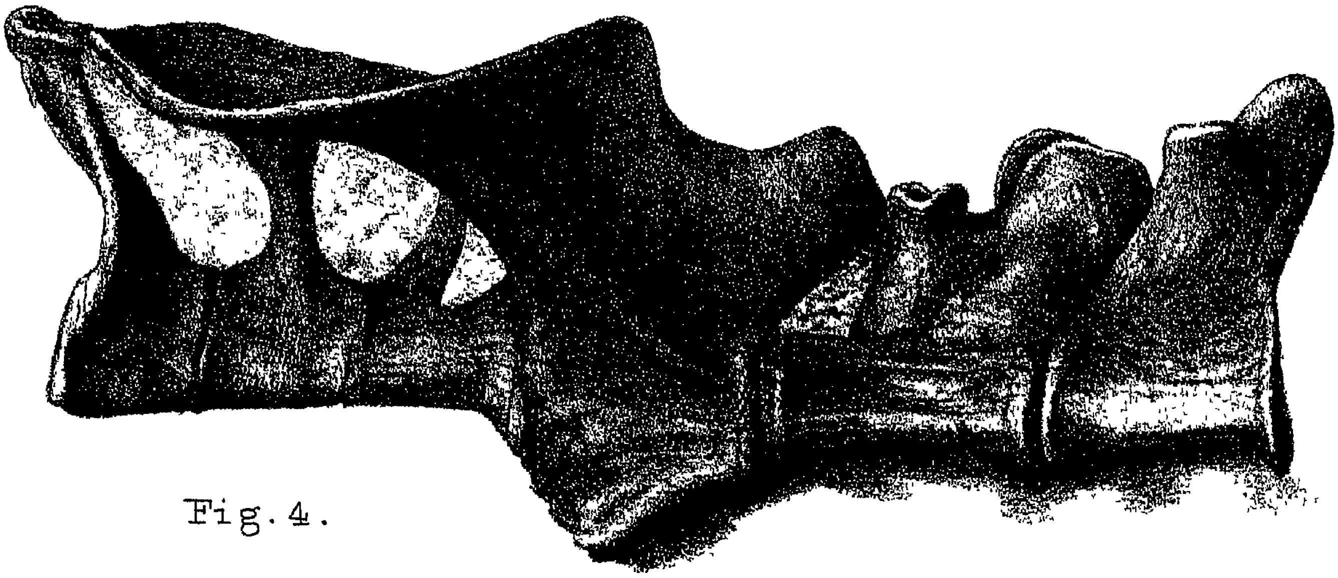


Fig. 4.

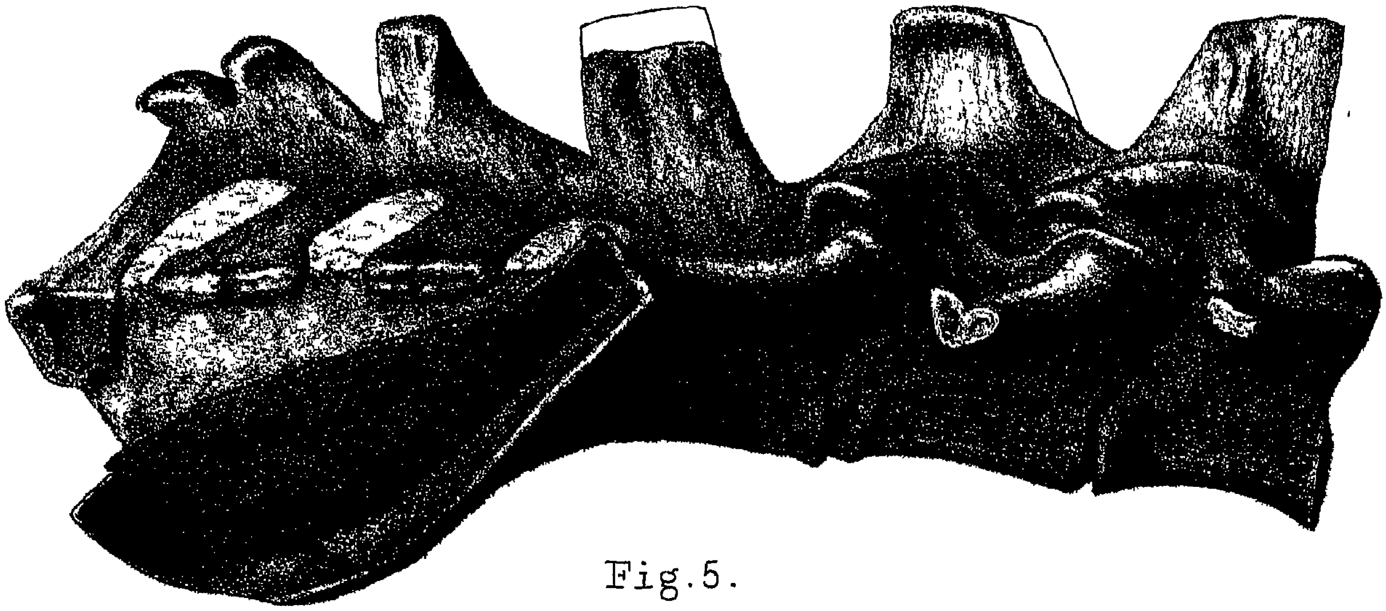


Fig. 5.

A.T. Hollick lith. West, Newman imp.

Sacrum and Vertebræ, *gen ?*

VIII. *The Physiological Action of the Nitrites of the Paraffin Series, considered in connection with their Chemical Constitution.*

By J. Theodore Cash, *M.D., F.R.S., Professor of Materia Medica in the University of Aberdeen, and* Wyndham R. Dunstan, *M.A., Professor of Chemistry to the Pharmaceutical Society of Great Britain.*

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Part II. Received June 15,—Read June 16, 1892.

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I.—Introduction.

The present investigation was commenced three years ago, in order to throw further light on the mode of action of the paraffinic nitrites when introduced into the animal organism, and particularly to determine in what manner this action is conditioned by the different chemical constitution of the various nitrites employed. Since the chemical constitution of these compounds is well established and their molecules are comparatively simple in structure, and moreover as their principal physiological effects are capable of accurate quantitative study, it seemed likely that the inquiry would furnish valuable pharmacological results. Although the investigation, both on its chemical and physiological sides, has proved to be far more laborious and difficult than was anticipated, unexpected difficulties having arisen which have rendered necessary the employment of specially-devised apparatus, and the execution of several series of experiments in order to control the accuracy of the results first obtained, yet the conclusions we have finally reached will serve, we think, not only to elucidate the modes of action of these compounds, and to establish the manner of their dependence on the presence of certain groups in the respective molecules, but we hope may also be of some importance in their bearings on the treatment of disease. It is already known that the physiological action of amyl and ethyl nitrites closely resembles in its important features that of the metallic nitrites, and that the characteristic effect is due to the presence in both series of compounds of the nitroxyl group NO_2, the nitrogen of this group not being directly united to the metal or organic radical, but indirectly by means of an atom of oxygen ($R'ONO$). Our knowledge of the physiological behaviour of the organic nitrites has been almost wholly derived from the study of amyl nitrite, which has been observed to produce a similar, but far greater, effect than its lower homologue, ethyl nitrite, whose action, however, has not hitherto been so closely examined as that of the amyl compound. Both these organic nitrites are therapeutically employed, the amyl compound at the suggestion of LAUDER BRUNTON, who proposed to use it in the treatment of certain diseases on account of its known physiological action. Unfortunately, however, it seems likely that most of the results which have been obtained with amyl nitrite are to a large extent vitiated by the circumstance that, as a rule, sufficient pains have not been taken to procure the nitrite in a chemically pure state.

One of us has already shown* that the material usually employed in medicine under the name of amyl nitrite is highly impure, containing a large proportion of other nitrites (ethyl, propyl, butyl), as well as their oxidation products. The redistilled amyl nitrite which has been employed by some investigators is a mixture of two amyl nitrites with a variable proportion of iso-butyl nitrite. In the present investigation special precautions were taken to obtain the various nitrites in a pure state. The compounds selected for examination were: methyl nitrite, ethyl nitrite, primary propyl nitrite, secondary propyl nitrite, primary butyl nitrite, iso-butyl nitrite, secondary butyl nitrite, tertiary butyl nitrite, α-iso-amyl nitrite, β-iso-amyl nitrite, tertiary amyl nitrite. These nitrites were chosen because they contain nitroxyl united to typical and differently constituted radicals. Their examination would, therefore, enable us to determine the modifying influence exerted by these radicals upon the characteristic action of nitroxyl.

Having concluded a complete investigation of the physiological action of these nitrites, we found that many of the results we had obtained were so remarkable, and in some respects contrary to what *primâ facie* seemed probable, that we determined to repeat all the most important experiments. This necessitated the preparation of fresh specimens of all the compounds.

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* DUNSTAN and WOOLLEY, "On the Constituents of the Amyl Nitrites used in Medicine." 'Pharm. Journ.' (3), vol. 19, p. 487.

After spending nearly the whole of the past year in this work of verification we had the great satisfaction of obtaining entire confirmation of our original results. In no instance was any important difference detected in the behaviour of these bodies.

In this, the first part of our communication, we shall give a short account of the principal work which has already been done on the subject, and shall then proceed to describe the methods by which the nitrites have been prepared and their purity ascertained. Of the numerous physiological experiments that have been made, we have selected for description such as are best suited to emphasize the peculiarities in the behaviour of these bodies. The physiological actions which we have made the subject of special study are those on blood pressure, pulse, and respiration, whilst we have also fully examined the action on striated muscular fibre. The first portion of the paper (Secs. III.–VII.) will deal almost entirely with the action of the various nitrites on blood pressure, and with the special apparatus used in its study. The latter part (Sec. VIII.) of the paper will have reference to the action of these same nitrites in producing contraction of striated muscle, and will conclude with a chemical discussion of the whole of our results.

The chemical part of this inquiry has been conducted in the Research Laboratory of the Pharmaceutical Society, and the physiological portion in the Pharmacological Laboratory of the University of Aberdeen.

The expenses of the research have been in part defrayed by grants made by the Royal Society and by the Scientific Grants Committee of the British Medical Association.

II.—Description of the Nitrites and of the Processes used in Preparing them.

The nitrites have been prepared by a process which has already been described, so far as it relates to the production of ethyl, iso-butyl, and amyl nitrites.* It consists in acting in the cold with dilute sulphuric acid and an excess of sodium nitrite on the corresponding alcohol previously obtained perfectly pure ($R'OH + HNO_2 = R'NO_2 + H_2O$). The alcohol is mixed with the well-cooled solution of sodium nitrite, and the dilute sulphuric acid gradually added; in some cases a mixture of the alcohol and acid is gradually added to the excess of sodium nitrite in aqueous solution. This has proved to be a satisfactory method for preparing the entire series of paraffinic nitrites with which we have worked. When secondary and tertiary alcohols have been used, it has been found desirable to employ acetic acid instead of sulphuric acid to bring about the reaction. The liquid nitrites, after having been thoroughly washed and dried, were repeatedly distilled, sometimes under reduced pressure, until a liquid boiling at a constant temperature was obtained. That the liquids thus obtained had the composition of the required nitrites was proved by determining the amount of iodine liberated by each compound from an acid solution of potassium iodide in the absence of oxygen, the operation being conducted in an apparatus specially devised for the purpose which has already been described.* In every case the precaution was taken of determining the physiological action of the nitrites almost immediately after their preparation, since most of these bodies suffer some decomposition when kept. The purity of each nitrite was thus ensured (1) by the employment of the pure alcohol in the first instance; (2) by the distillation of the liquid at a constant temperature; (3) by the results of a particularly delicate process of analysis. The composition of each nitrite was in this way determined with greater accuracy than would have been possible by the usual method of determining the amount of nitrogen by combustion.

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* Dunstan and Dymond, "On the Preparation of Ethyl Nitrite." 'Pharm. Journ.' (3), vol. 19. Dunstan and Woolley, "On Iso-butyl Nitrite." 'Pharm. Journ.' (3), vol. 19, p. 487. Dunstan and Williams, "On the Metameric Amyl Nitrites." 'Pharm. Journ.' (3), vol. 19, p. 488.

The following are the names, formulæ, and boiling-points of the nitrites with which we have worked:—

Name.	Formula.	Boiling-point.
Methyl nitrite	CH_3NO_2	Gas (12°)
Ethyl nitrite	$CH_3CH_2NO_2$	17°
Primary propyl nitrite	$CH_3CH_2CH_2NO_2$	48°
Secondary propyl nitrite	$(CH_3)_2CHNO_2$	39°·5
Primary butyl nitrite	$C_2H_5CH_2CH_2NO_2$	76°
Secondary butyl nitrite	$C_2H_5CH_3CHNO_2$	68°·5
Tertiary butyl nitrite	$(CH_3)_3CNO_2$	63°
Iso-primary butyl nitrite	$CH_3CH(CH_3)CH_2NO_2$	67°
α-iso-primary amyl nitrite	$CH(CH_3)_2CH_2CH_2NO_2$	97°
β-iso-primary amyl nitrite†	$C_2H_5CH(CH_3)CH_2NO_2$	95°–96°
Tertiary amyl nitrite	$C_2H_5(CH_3)_2CNO_2$	92°

Certain of these nitrites were prepared by us for the first time,‡ whilst of those previously described some have been found to possess physical properties differing from those usually ascribed to them. For the purpose of administration a known volume of each nitrite was taken, and in the description of the experiments the weight corresponding to the volume is given in brackets, as well as the weight of nitroxyl (NO_2) contained in the quantity of the substance administered, this weight being calculated from the molecular weight and the relative density of the compound.

The preparation, purification, and analysis of these nitrites has been a most laborious and tedious undertaking, and we wish to express our great indebtedness to

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* DUNSTAN and DYMOND, "On an Apparatus for the Estimation of Nitrites." 'Pharm. Journ.' (3), vol. 20.

† These two amyl nitrites are subsequently called for shortness α-amyl and β-amyl respectively.

‡ Some of them have since been prepared by BERTONI.

Miss LUCY EVEREST BOOLE for the able assistance she has rendered us in carrying out this work.

Methyl Nitrite, CH_3NO_2.—This nitrite, which is a gas at ordinary temperatures, was prepared by the reaction of aqueous sodium nitrite and pure methyl alcohol with dilute sulphuric acid. The quantities used were calculated from the chemical equation, the sodium nitrite being employed in slight excess. The alcohol and the acid were each diluted with an equal volume of water, and, after having been well cooled, were gradually mixed. This mixture was allowed to slowly drop from a tap-funnel into a solution of sodium nitrite (made by dissolving the salt in about three times its weight in water) contained in a flask cooled by water. Methyl nitrite was immediately formed and passed forward into a U-tube filled with quicklime cooled by ice. In this way the gas was freed from acid vapour and from water. It was found, however, on analysis, to be contaminated with small quantities of nitric oxide. In order to obtain it free from this impurity the gas, on emerging from the U-tube, was conducted into well cooled methyl alcohol until the liquid was completely saturated. On warming this solution methyl nitrite was copiously evolved. The gas was freed from the accompanying vapour of methyl alcohol by passing it through the U-tubes, containing porous calcium chloride cooled to 0°. For the purpose of analysis some of the gas was collected in a gas analysis apparatus over dry mercury, and from thence a known volume was introduced into the apparatus in which its iodine liberating power was ascertained.

The results of the analysis showed the gas thus prepared to be pure methyl nitrite (weight of methyl nitrite, corresponding to the volume taken, = 0·0951 grm.; weight of methyl nitrite, calculated from iodine liberated, = 0·0953 grm.). The gas was collected in thin glass bulbs of known capacity (2–10 cub. centims.), a series of such bulbs being connected with the generating and drying apparatus above described, and a current of gas passed through until the whole of the air was completely expelled, as evidenced by the entire absorption of the escaping gas in well-cooled methyl alcohol. The last bulb of the series was provided with a fine extremity, which dipped into the cooled alcohol. As soon as the minute bubbles of escaping gas were completely absorbed the two ends of each bulb were quickly sealed with a small flame. The temperature and pressure having been observed during the process, the weight of methyl nitrite contained in each bulb was readily calculated, and, in order to be quite certain that the proper quantity of methyl nitrite was actually present, one or two of the bulbs selected from each series were broken and the quantity of contained nitrite estimated by analysis.

Ethyl Nitrite, $C_2H_5NO_2$.—The method of preparing this compound in a pure state has already been described in a previous paper.* A mixture of dilute sulphuric acid and pure ethyl alcohol was caused to react at a low temperature with a solution of sodium nitrite. The sodium nitrite solution having been cooled to 0°, the mixture of dilute acid and alcohol is gradually introduced through a thistle funnel to the bottom of the cold solution of the salt. Under these circumstances there rises to the surface the pale yellow liquid nitrite, which is washed, dried (with potassium carbonate), and distilled. The sodium nitrite is employed in slight excess to prevent the nitrite from coming into contact with dilute sulphuric acid, which readily decomposes it. The pure liquid boils at 17° (barometric pressure, 760 millims.), and its relative density is 0·900 at 15°/15°.

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* DUNSTAN and DYMOND, "On the Preparation of Ethyl Nitrite," 'Pharm. Journ.' (3), vol. 19, p. 7.

Primary Propyl Nitrite, $C_2H_5CH_2NO_2$.—This compound was prepared by the reaction of a mixture of sulphuric acid and pure primary propyl alcohol with aqueous sodium nitrite, the operation being conducted as in the preparation of the ethyl compound. The quantities taken were calculated from the equation, the sodium nitrite being used in slight excess. The greater part of the liquid distilled constantly at 48° (barometric pressure, 761·8 millims.). Its relative density was 0·895 at 15°/15°. Analysis proved it to be propyl nitrite: the nitrite was weighed into propyl alcohol, and the iodine-liberating power of the liquid ascertained. (Weight of propyl nitrite taken, 0·2062 grm.; weight of propyl nitrite calculated from the amount of iodine liberated, 0·2063 grm.).

The physical constants usually assigned to this compound differ very considerably from those we have found for the liquid prepared as above described. Its discoverer, CAHOURS ('Comptes Rend.,' vol. 77, p. 745), states that it boils between 43° and 46°; its relative density at 21° being 0·935. PŘIBRAM and HANDL ('Monatshefte' 2, p. 655) have recorded 53°–60° (barometric pressure, 736 millims.) as the boiling-point, and 0·9981 as the relative density at 0°. More recently BERTONI and TRUFFI ('Gazz. Chim. Ital.,' vol. 14, p. 23) have obtained primary propyl nitrite by acting on iso-amyl nitrite with primary propyl alcohol. They state that it boils at 57°.

In order to obtain confirmatory evidence of the correctness of our results, the nitrite was prepared by an entirely distinct method, viz., by the reaction of primary propyl iodide with silver nitrite. The resulting mixture of primary propyl nitrite and primary nitropropane was fractionally distilled. By this means the nitrite was obtained, and found to correspond exactly with that we had prepared from the alcohol as above described.

Secondary Propyl Nitrite, $CH_3CH_2CHNO_2$.—This nitrite was obtained by acting on pure secondary propyl alcohol with dilute sulphuric acid and solution of sodium nitrite, the details of the method being similar to those described in connection with ethyl nitrite. A liquid was obtained which boiled constantly at 39°·5 (barometric pressure, 752 millims.). Its relative density was 15°/15° 0·871. Analysis proved it to be secondary propyl nitrite. (Weight of nitrite taken dissolved in the alcohol, 0·1899 grm.; weight of nitrite calculated from the amount of iodine liberated, 0·190 grm.) According to SILVA ('Bull. Soc. Chim.,' vol. 12, p. 227) secondary propyl nitrite boils at 45°, whilst KISSEL ('J. Russ. Chem. Soc.,' vol. 14, p. 229) alleges that another modification is formed by the reaction of secondary propyl iodide with silver nitrite, which boils at about the same temperature, but more closely resembles a nitro-compound than a nitrite. Owing to these discrepant statements we determined to compare the properties of the nitrite resulting from the reaction of the iodide and silver nitrite with those of the nitrite we had obtained. Pure secondary propyl iodide was caused to react with dry silver nitrite, the operation being conducted in a manner described by one of us in a previous paper on the reaction between ethyl iodide and silver nitrite.*

A liquid was obtained which boiled constantly at 39°·5, and corresponded exactly with the nitrite we had obtained from the alcohol.

Nothing else could be obtained from the original liquid except secondary nitropropane. No trace of any such substance as that described by KISSEL could be isolated.

Primary Butyl Nitrite, $C_2H_5CH_2CH_2NO_2$.—This nitrite was prepared by the reaction of a mixture of pure primary butyl alcohol and dilute sulphuric acid, with a slight excess of solution of sodium nitrite. The details of the operation are precisely similar to those followed in the preparation of the nitrites previously described. A large quantity of a pale yellow liquid was obtained, which distilled constantly between 75°–76° (barometrical pressure, 757 millims.). It was identified as primary butyl nitrite by estimating the amount of nitrous group contained in a weighed quantity of the liquid dissolved in butyl alcohol (weight of nitrite taken, 0·1513 grm., weight of nitrite calculated from the amount of iodine liberated, 0·1512 grm.). Its relative density was 0·891 at 15°/15°. This nitrite is one of the most unstable of those prepared. It was found impossible to keep it unchanged for any length of time. It has been prepared by BERTONI ('Gazz. Chim. Ital.,' vol. 18, p. 434) by acting on glyceryl trinitrite with primary butyl alcohol. He states that it boils at 75°, and has at 0° a relative density of 0·911.

Secondary Butyl Nitrite, $C_2H_5CH_3CHNO_2$.—We attempted to prepare this nitrite by the reaction of pure secondary butyl alcohol (obtained by the reduction of ethyl methyl ketone), with dilute sulphuric acid and excess of sodium nitrite. It was found difficult by this method to obtain any considerable quantity of liquid distilling at a constant temperature. A more abundant product resulted from the substitution of strong acetic acid for dilute sulphuric acid and the use of less water to dissolve the sodium nitrite, but under these circumstances the reaction is much slower. The secondary nitrite thus prepared boils at 68°·5 with some decomposition. Its relative density at 15°/15° was 0·874. Its analysis proved it to be secondary butyl nitrite (weight of nitrite taken 0·1602 grm., weight of nitrite calculated from the amount of iodine liberated, 0·1587 grm.). BERTONI ('Gazz. Chim. Ital.,' vol. 18, p. 435) has recently prepared this nitrite by acting on glyceryl trinitrite with secondary butyl alcohol. He found its boiling point to be 68°, and its relative density at 0°, 0·898.

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† DUNSTAN and DYMOND, "On the Alleged Existence of a Second Nitro-ethane," 'Chem. Soc. Journ.,' 1889.

Tertiary Butyl Nitrite, $(CH_3)_3CNO_2$.—This nitrite was found to be best prepared by the modification of the general process described in connection with secondary butyl nitrite, acetic acid being substituted for dilute sulphuric acid. By this means a yellow liquid was obtained which boiled with slight decomposition at 63° (barometrical pressure, 760 millims.). In purifying it, distillation under reduced pressure was resorted to. Its relative density was found to be 0·8715 at 15°/15°. The compound when analysed yielded the following result (weight of nitrite taken dissolved in the alcohol, 0·203; weight of nitrite calculated from the amount of iodine liberated, 0·205). This nitrite was first obtained by TSCHERNIAK ('LIEBIG'S Ann.,' vol. 180, p. 155), by acting on silver nitrite with tertiary butyl iodide. He states that it boils at 76°–78°. The correctness of our results with this nitrite have been confirmed by those obtained by BERTONI ('Gazz. Chim. Ital.,' vol. 15, p. 358), who prepared the compound by the interaction of glyceryl trinitrite with tertiary butyl alcohol. The resulting liquid boiled at 62°–63°, and its relative density at 0° was 0·8941. There can therefore be no doubt that the higher boiling-point recorded by TSCHERNIAK was due to the nitrite having been contaminated with the corresponding nitro-compound which was formed simultaneously.

Iso-Butyl Nitrite, $CH_3CH(CH_3)CH_2NO_2$.—The mode of preparing this nitrite by the reaction of pure iso-butyl alcohol, dilute sulphuric acid, and sodium nitrite has already been described by one of us.* A large yield of the pure substance is readily obtained. It boils at 67° (barometric pressure, 760 millims.), and its relative density at 15°/15° is 0·876. When analysed it afforded the following result (weight of nitrite taken, 0·1513 grm.; weight of nitrite calculated from the amount of iodine liberated, 0·1512 grm.). BERTONI ('Gazz.,' vol. 14, p. 23) records 66°–67° as the boiling point of this nitrite.

α-Amyl Nitrite, $CH(CH_3)_2CH_2CH_2NO_2$.—This nitrite was first prepared in a pure state and described by one of us in 1888.† The pure α-amyl alcohol or iso-butyl carbinol, the optically inactive amyl alcohol of fusel oil, was separated from the mixture of α-amyl alcohol and β-amyl alcohol (fusel oil) by PASTEUR'S method of repeatedly crystallizing the two barium amyl sulphates. The process was a most laborious one, necessitating the recrystallization of the barium salts from water thirty-four times in succession, in order to completely remove the more soluble salt corresponding to β-amyl alcohol, the optically active alcohol of fusel oil. The nitrite was prepared by reaction with sulphuric acid and sodium nitrite. The compound distilled constantly at 97° (barometric pressure, 758·5 millims.). The relative density at 15°/15° is 0·880. Analysis showed the liquid to possess the composition of α-amyl nitrite (weight of nitrite taken 0·178 grm.; weight of nitrite calculated from the amount of iodine liberated 0·179 grm.).

β-Amyl Nitrite, $C_2H_5CH(CH_3)CH_2NO_2$.—This nitrite which corresponds to β-amyl alcohol or secondary butyl carbinol the optically active alcohol of fusel oil was not isolated in an absolutely pure state. Its physiological action was ascertained by examining the nitrites prepared from a mixture in known proportions (calculated from the rotatory power of the mixture of β-amyl alcohol and α-amyl alcohol) the physiological action of the α-amyl nitrite having been previously ascertained. It is doubtful whether pure β-amyl alcohol has yet been obtained, since the numbers representing the optical activities of specimens prepared by different observers are very discordant. For the purposes of our calculations, we have adopted the number found by LE BEL, whose alcohol produced a greater rotation than that of any other observer ($\alpha_D = 4° 58''$).

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* DUNSTAN and WOOLLEY, "On Iso-Butyl Nitrite." 'Pharm. Journ.' (3) vol. 19, p. 487.

† DUNSTAN and WILLIAMS, "On the Metameric Amyl Nitrites." 'Pharm. Journ.' (3), vol. 19, p. 488.

We have found that the nitrite prepared from this lævo-rotatory alcohol by the action of dilute sulphuric acid and sodium nitrite is dextro-rotatory. The nitrite boils between 95°–96°, and appears to possess a smaller relative density than the α-nitrite.

Tertiary Amyl Nitrite, $C_2H_5(CH_3)_2CNO_2$.—An attempt was made to prepare this nitrite by the interaction of the pure alcohol with dilute sulphuric acid and sodium nitrite. The reaction was extremely violent, even at a low temperature, and only a very small yield of a homogeneous liquid was obtained. By repeating the process and substituting strong acetic acid for dilute sulphuric acid a much better result was obtained. The alcohol was mixed with a solution of sodium nitrite dissolved in the necessary quantity of water, and the strong acetic acid (glacial acetic acid diluted with half its volume of water) gradually added. The reaction occurred slowly, and in order to facilitate it the mixture was transferred to a bottle and well shaken. The yellow layer of nitrite was then decanted and washed. The substance was observed to be decomposed by prolonged contact with water or by digestion with potassium carbonate, which therefore could not be used to dry it. To remove traces of acid from the liquid, a small fragment of calcium hydroxide was added, and to remove water the liquid was digested with anhydrous calcium nitrate. On distilling it under reduced pressure, a large quantity of liquid was obtained between 30°–31°; under atmospheric pressure the nitrite boiled at 92°, with some decomposition. Its relative density was 0·890 at 15°/15°. Analysis showed that the composition of this liquid corresponded with the formula of tertiary amyl nitrite (weight of nitrite taken, 0·184 grm.; weight of nitrite calculated from the amount of iodine liberated, 0·182 grm.). Tertiary amyl nitrite is one of the most difficult of the series to obtain pure, and it cannot be kept without suffering decomposition. BERTONI ('Gazz. Chim. Ital.,' 16, 515) has recently prepared this compound by acting on tertiary amyl alcohol with glyceryl trinitrite. He states that it boils at 92°–93°, and has at 0° a relative density of 0·903.

III.—ACTION OF AMYL NITRITE ON THE BLOOD PRESSURE. DESCRIPTION OF THE METHOD OF INVESTIGATION.

The large amount of attention which has been bestowed on the action of nitrite of amyl during the last thirty years, has established certain facts regarding it which are recognised on all hands; but it has left us in considerable doubt as to the occurrence of other phenomena which are described by some investigators, but questioned by others. The explanation of even the most evident nitrite effect, viz., the fall of blood pressure, is still disputed.

The principle observed in the experiments, which it seemed advisable to make, in order to obtain further information on the action of nitrates, has been to carefully analyse and contrast the effect produced by exactly measured quantities of the pure bodies upon the whole organism, or certain of its tissues.

After briefly sketching the history of previous investigations with the so-called amyl nitrite, in so far as they bear upon the scope of our inquiry, the action of pure nitrite of amyl will be discussed in detail, in order that its effects may serve as a basis for contrast with the bodies which will be considered in a later portion of this paper.

History.

Nitrite of amyl, discovered in 1844 by BALARD,* was examined in 1859 by GUTHRIE,† who showed that its inhalation was followed by reddening of the face, and acceleration with alteration in form of the pulse. RICHARDSON‡ confirmed the occurrence of capillary dilatation (68); GAMGEE§ observed a fall in the blood-pressure, and, in 1873, AUREZ DROZ measured it; BRUNTON,‖ in 1871, endeavoured to show that the seat of direct action of the drug is in the walls of the vessels, and observed that vagotomy increased its effect. FILEHNE¶ opposed BRUNTON'S view, and regarded the action as primarily central.

Amongst those who have supported BRUNTON'S views are PICK,** WOOD,†† MAYER,‡‡ and FRIEDRICH.§§ AUREZ DROZ,‖‖ it is true, localises the nitrite action at the periphery, but refers it to the nerve terminations there. On the other hand,

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* 'Ann. d. Phys. Nml. et Path.,' 1873.

† 'Ann. d. Chem. et Pharm.,' v. 3.

‡ 'Trans. Brit. Med. Assoc.,' 1864–72.

§ 'Phil. Trans.,' 1868.

‖ 'Journ. of Anat. and Phys.,' v. 5.

¶ PFLÜGER'S 'Arch.,' v. 9, p. 471.

** 'C.-Blatt. Med. Wis.,' 1873, p. 865.

†† 'Amer. Journ. Med. Sci.,' July, 1871.

‡‡ 'Arch. f. Exp. Path. u. Pharm.,' v. 5, 63.

§§ 'Arch. f. Exp. Path. u. Pharm.,' v. 5, 76.

‖‖ 'Arch. d. Phys.,' 1873, p. 407.

FILEHNE is in part supported by BERNHEIM, GUTTMANN, MCBRIDE, and KEMPTON in his contention that the first effect of the drug is a central nervous paralysis.

The "capillary dilatation" (as it is usually designated by authors) was especially studied by RICHARDSON and by MAX SCHÜLLER in the pia mater, by GASPY in the rabbit's ear, by AUREZ DROZ in the swim-membrane of the frog; but it was not recognised locally by GAMGEE and MCBRIDE[*] when observing the forearm or leg. FILEHNE saw no reddening of the lungs; and PICK failed to detect retinal pulsation under nitrite action.

A slowing of respiration followed by acceleration with diminution of thoracic movement was observed by VERGRIERES, BOURNEVILLE,[†] and CRICHTON BROWNE.

An acceleration of the heart of animals was seen by almost all experimenters, including WOOD, who stated that nitrite of amyl accelerated the heart by direct action, whilst others attributed the change to suspension of vagus tonus. But these observations were questioned by FILEHNE, who pointed out that in frogs and other animals to which the nitrite had been repeatedly given, slowing of the heart was produced.

The poisonous action of the nitrite of amyl upon muscle is mentioned by WOOD—who recognized it as a paralysant both in the fluid and vaporous form,—by BRUNTON with GRESSWELL,[‡] and by PICK,[§] the last of whom exposed curarised muscles to nitrite of amyl vapour, and found that they completely lost excitability; whilst spinal paralysis is described by WOOD, convulsions by BRUNTON and others.

BRUNTON, GAMGEE, HAY,[||] GIACOSA,[¶] JOLYET, and REYMOND,[**] with others, discuss the chemical changes produced in the blood by nitrite action. The reduction of body temperature has been widely recognized by experimenters as a nitrite effect.

Amongst those who have, by clinical study, extended our knowledge concerning the action of nitrite of amyl, need only be mentioned here: LAUDER BRUNTON, who showed its curative effects in angina pectoris; WEIR MITCHELL,[††] who wrote upon its favourable effects in epilepsy; Drs. CRICHTON BROWNE and BOURNEVILLE,[‡‡] who made observations in the same direction; and ANSTIE, who employed it in gastric spasm.

The names of RICHARDSON, TALFOURD JONES, RINGER with MURRELL and MACCULLOCH, must also be remembered in connection with the investigation of the therapeutical and antidotal action of this drug or its allies, whilst the important and most recent contributions on ethyl nitrite by LEACH and by FRASER must be borne in mind, as illustrating the therapeutic value of these compounds.

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[*] 'Chicago Journ. of Nerv. and Mental Dis.,' 1875.

[†] 'Gaz. Méd. d. Paris,' 1876, p. 150.

[‡] 'St. Barts. Hosp. Reports,' 1876, p. 143.

[§] 'Centralbl. d. Med. Wis.,' Berlin, 1873.

[||] 'Practitioner,' June, 1883.

[¶] 'Zeitsch. f. Physiol. Chem.,' vol. 3, p. 54.

[**] 'Gaz. Méd. de Paris,' 1875.

[††] 'Phil. Med. Times,' 1872, p. 353.

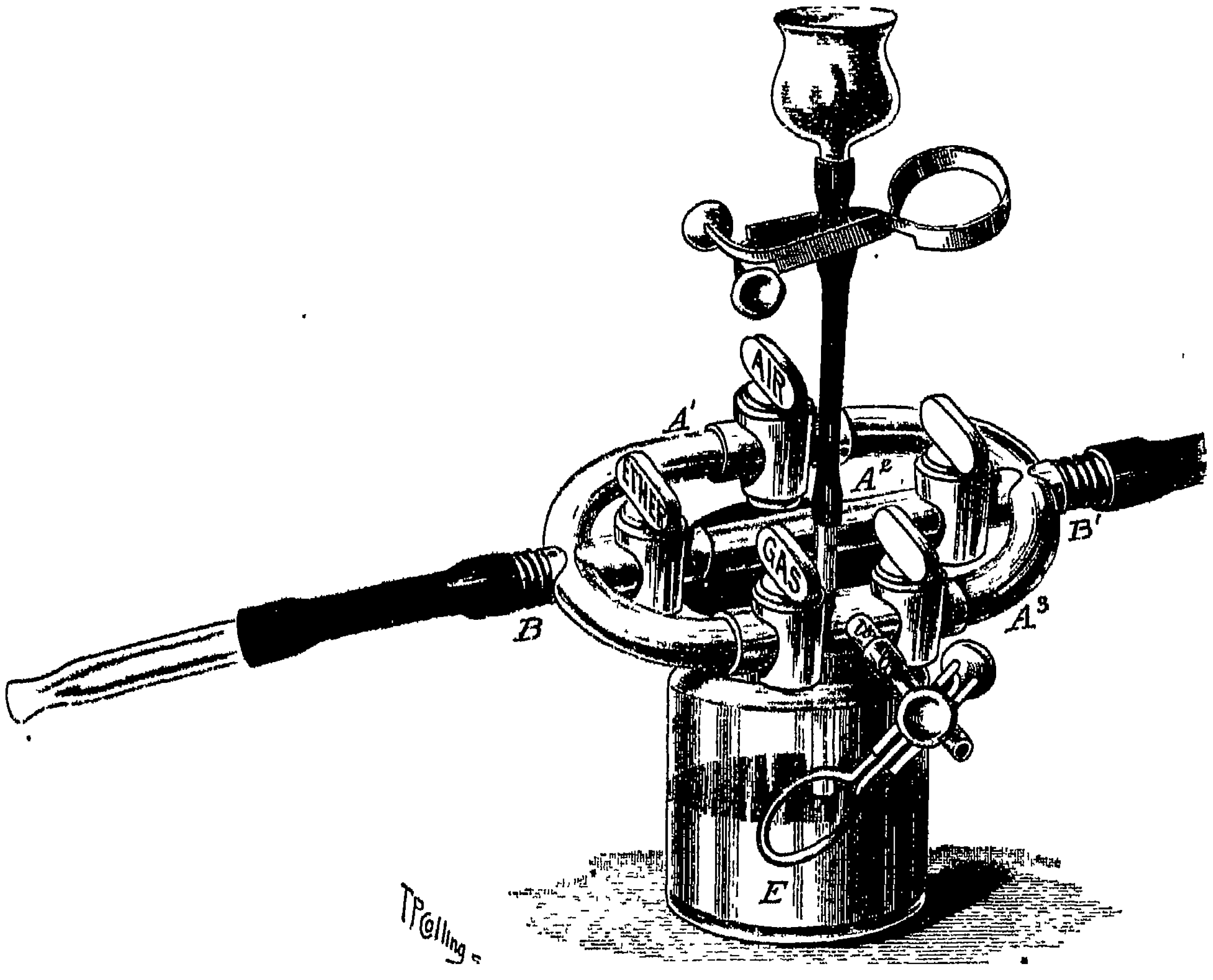
[‡‡] 'Gaz. Méd. de Paris,' 1876.

Methods Employed in the Investigation.

The difficulty in following exactly the results obtained by many observers who have experimented upon the action of nitrites, is owing not only to the doubtful purity of the nitrite employed, but partly also to the scanty idea conveyed as to the actual amount inhaled by the individual or animal experimented upon.

Supposing that, according to the usual custom, "a few drops" have been poured upon some fabric, and held near the mouth and nose; it would follow that, according to the actual distance of the drug from the face, the activity of respiration, the temperature of the room, and the volatility of the nitrite employed, a larger or smaller amount (we can hardly say approximately how much) would be inhaled and produce the various effects upon respiration, heart, and peripheral vessels, and even upon the central nervous system, which are recorded as nitrite effects. In order to obviate such discrepancies as must arise from want of uniformity in the dose, a special apparatus was used in this research for administering nitrites by inhalation through the nostrils in the human subject, and another for administration through the trachea in animals. The former will be described in a subsequent section. The latter (fig. 1) consisted of three short tubes, A^1, A^2, A^3, of equal diameter, somewhat greater than the trachea of a large cat, permanently connected by means of two common or main tubes (B and B^1) to which they converged at their ends. One of the three tubes (A^1) had no further connection; the second (A^2) passed through the stopper of the ether bottle (E) without dipping (somewhat as in BRUNTON'S special apparatus for administration of anæsthetics); the third (A^3) resembled the first, but had a smaller brass tube (a) introduced at a right-angle. Two stop-cocks, one on either side of (a), were placed in the course of the large tube A^3. Through the tube A, when provided with a continuation of india-rubber (b) and a clamp, the nitrite could be discharged from the graduated pipette, a small fraction of a minim of water being introduced behind it to insure its entire washing out. In the greater number of experiments, instead of introducing the nitrite directly through the lateral tube into the partition between the stop-cocks, a spindle-shaped bulb, closed by tubing clamped at each end, was brought into connection with it, the nitrite having been previously introduced into the bulb. In the nitrite of methyl experiments, in which the body was in a gaseous state, the same plan was followed, the hermetically sealed ends of the bulb being broken before the stop-cock giving access to the tracheal cannula was opened. Distal to the bulb in all cases was a water valve which permitted ingress but not egress of air. A similar valve was placed in connection with the common tube B. The tracheal cannula was provided laterally with a valve permitting exit but not entrance of air. When all the stop-cocks in the apparatus (fig. 1) were closed, with the exception of the one nearest the animal in tube A^3, and the clamps on the bulb were unscrewed, the whole of the nitrite was inhaled, the water valve preventing loss upon expiration. For the continued administration of the anæsthetics it was usually found sufficient to have the air tube partially and the ether tube fully open, so that inhalation could take place through both of them simultaneously. The adjustment to produce steady but not excessive etherisation was made before the experiment commenced, and was usually adhered to throughout.

Fig. 1.

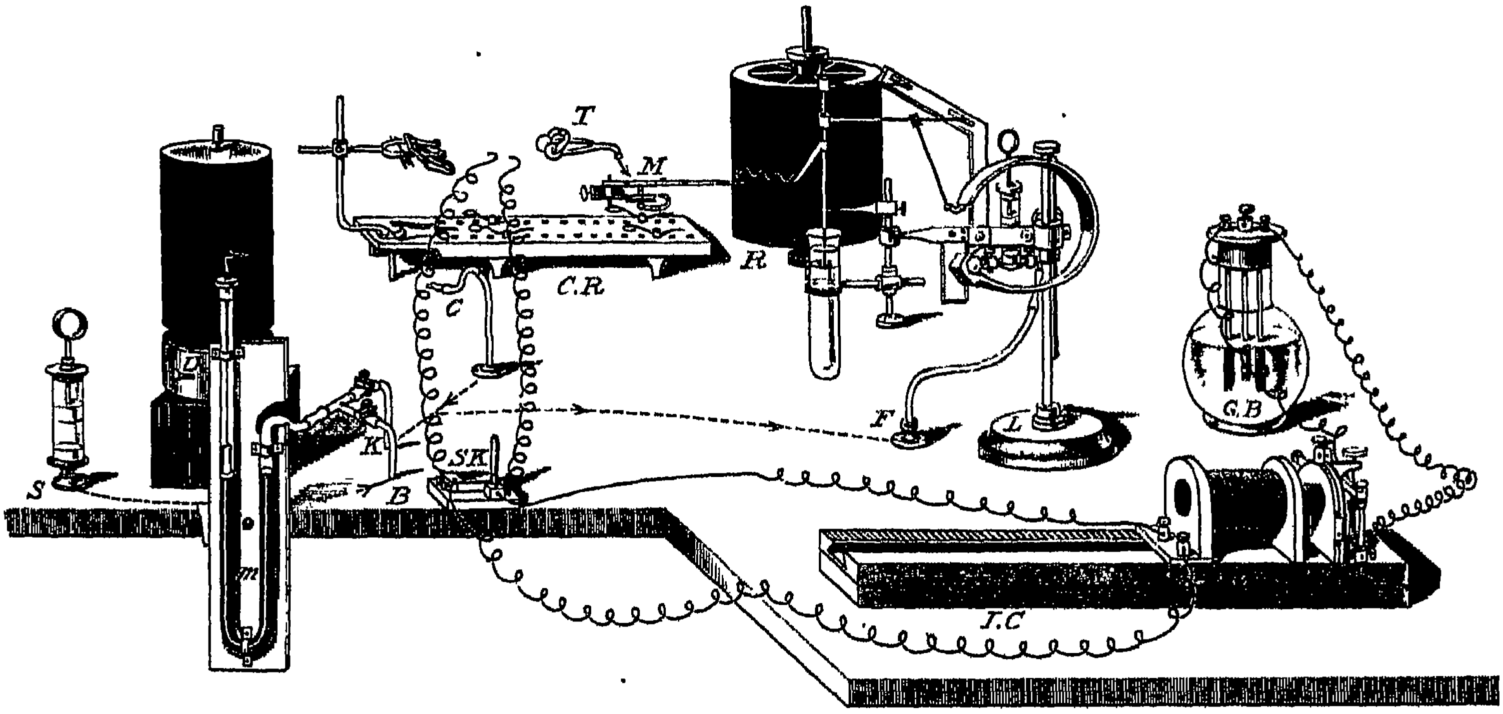


Apparatus for administration of an anæsthetic or other volatile bodies (one-half actual size). For description, see text.

At the moment of nitrite inhalation, the first intermediate tube (A^1), which was used for air supply alone, as well as the proximal ether tube (A^2), were turned off, and the nitrite tube (A^3) opened. The special valvular arrangement which has been described did not permit the expired air to return to the tube apparatus, so that there was no loss of the nitrite during expiration, and practically the whole amount entered the trachea.

Absolutely exact measurements of the nitrite were made by means of fine capillary glass pipettes, very carefully graduated. The bulk was thus ascertained, and the weight subsequently determined from the relative density. One pipette was used for a given dose throughout an experiment; it was thoroughly cleansed between every two measurements by washing with water, then with alcohol, and finally drying by heat. The recording apparatus (fig. 2) for the blood-pressure was arranged much in the same way as in experiments made conjointly by Dr. LAUDER BRUNTON and one of us. (C.) It consisted of a mercurial manometer writing upon a slowly revolving drum (one revolution in one hour), and a Fick's kymograph, writing upon a more rapidly revolving Balzar's cylinder. These manometers could be employed separately by clamping one of them off, but as a rule, when only pressure and number of pulsations were being observed, both were kept open. The advantage of this arrangement is that a considerable period of time is represented by a short lineal movement on a small drum, while on the quick cylinder the pulse can be reckoned, and the course of the rapidly occurring variations of pressure studied.

Fig. 2.



Arrangement of apparatus used in blood-pressure experiments (partly diagrammatic). For description see text.

Respiration was recorded on the rapid cylinder by a registering Marey's tambour, attached to a double tambour placed upon the thorax of the animal. An electrical signal in connection with a key and Daniell's element was placed beneath the point recording the blood-pressure, in order to mark the time of administration of nitrites, &c. For the purpose of simplifying the apparatus in some experiments, the marking was done manually by an assistant, whose entire charge it was.

When vagus, splanchnic, or sciatic stimulation was employed, a double key admitted the Faradic current from the secondary coil of a Du Bois-Reymond's inductorium to the electrodes under the nerve, and at the same time it closed the signal circuit, and thus indicated the length of stimulation. Natural respiration was allowed to continue so long as it was unimpaired, but to secure regular volatilization of the nitrite, artificial respiration was substituted whenever the respiration became distinctly abnormal. It was also, of course, employed when preparation of the splanchnic nerves in the thorax necessitated resection of the ribs.

The course of a simple nitrite administration was the following:—When the blood-pressure was steady, the clockwork of the big drum was started, to bring it up to full speed before the cylinder was caused to rotate, by screwing up the friction wheel. The nitrite was then introduced into the side tube (fig. 1) of the inhaler, or into the bulb connected with this tube, both of the stop-cocks on A^3 and the clamp on *b* being closed. The cylinder was then started, and after a sufficient record of the pulse and respiration had been taken, the nitrite was given, the time of administration being recorded. During administration the tube A^2 was usually closed. After a sufficient time had been allowed for its inhalation (complete volatilization of the small amounts of the nitrite employed was found to take place in a very few inspirations), the air and ether tubes, if these had been closed, were re-opened, and the quick drum permitted to run as long as necessary for obtaining a full record of the changes in pulse and pressure. During the subsequent recovery of pressure, an occasional record of pulse and respiration was taken on the quick drum; corresponding marks being made on the slow drum.

Action of α-Amyl Nitrite on Blood-Pressure.

On all hands it is admitted that moderate doses of the nitrites hitherto examined cause a fall of blood-pressure, resulting chiefly, if not entirely, from a marked dilatation of the arterioles greatly reducing the peripheral resistance.

In explaining the cause of this dilatation, a divergence of opinion is observable. FILEHNE may be considered the chief authority who has striven to demonstrate experimentally that they act on the vaso-motor centre or centres. On the other hand, BRUNTON and MAYER with FRIEDRICH[*] maintain that their chief action is direct, on the walls of the vessels, and does not depend on a central effect. MAYER and FRIEDRICH by using the manometer found in the rabbit (1) that when the circulation was cut off from the brain and artificial respiration maintained, the blood-pressure still sank during inhalation of amyl nitrite; and (2) that when it had access to the brain alone, no fall of pressure ensued.

FILEHNE,[†] experimenting upon rabbits, and observing the dilatation of the auricular vessels as indicating the action of the drug, arrived at the following chief results:—(1) That if the sympathetic nerve be cut on one side of the neck, and then stimulated by an interrupted current so as to maintain a normal degree of vascular contraction in the ear, the nitrite does not produce vascular dilatation on that, but on the other side. (2) If the vessels of one ear are isolated and artificial circulation maintained in them, while their nerves remain undisturbed, the nitrite, when inhaled, still dilated the vessels of the ear to which it had no access. He therefore concluded that the dilatation results from paralysis of the vaso-motor centre.

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[*] MAYER, FRIEDRICH: 'Archiv f. Exp. Path. und Phys.,' vol. 5, p. 76.

[†] FILEHNE, "Die Wirkungen des Amyl-Nitrites." 'Archiv f. Anat. u. Phys.,' vol. 79, p. 384.

It appeared important to study in the first instance the points at issue between these authors. The necessary experiments were performed chiefly on cats, but in control experiments rabbits were used, and yielded almost the same results.

Experiment A.—Ether administered steadily to a cat from the bottle devised for nitrite inhalation, and complete, but not profound, anæsthesia maintained throughout the experiment. The upper portion of the sternum and three upper ribs on each side having been removed, a cannula was placed in the carotid of the right side, and the right vertebral artery ligatured, whilst the carotid and the subclavian artery on the left side were placed on threads so that at any time they could be drawn forward and clamped by bull-dog forceps covered with rubber. A cannula was also placed in the cranial end of the right carotid, and artificial respiration was steadily maintained. On clamping the left subclavian and carotid arteries, a rise of blood-pressure with slowing of the pulse very rapidly ensued, probably owing to vascular constriction arising from stimulation of vaso-motor and cardio-inhibitory centres. A rapid and considerable fall of pressure ensued when the vessels were liberated.

On administering $\frac{1}{38}$ cub. centim. (0·0231 grm.; $NO_2 = 0{\cdot}0091$ grm.) of pure nitrite of amyl by inhalation, the arteries being left open, a fall of pressure with subsequent pulse acceleration was recorded in ordinary course.

After a pause of 15 minutes, a record was taken of the normal pulse. The left subclavian and carotids were then clamped, so that the head was entirely cut off from the circulation. The blood-pressure first rose slightly and then remained stationary; $\frac{1}{38}$ cub. centim. of pure nitrite of amyl was now administered by inhalation; a rapid fall of pressure soon made its appearance, the lowest point being reached 35 seconds after inhalation commenced, this being almost exactly the point at which it occurred in the previous inhalation. The pressure then rose rapidly to a point considerably above the original level, but declined again slightly on the liberation of the carotid and subclavian; the decline was never to the same low level as during the administration of the nitrite when the brain was cut off from the circulation.

Experiment A.

Time.	Pulse.	Pressure.
secs.	In 1 minute.	In millims. Hg.
0	141	90
15 Ligatured subclavian	138	95
40 Ligatured carotid	111	92
50 75 } Inhale $\frac{1}{38}$ cub. centim. pure amyl nitrite	96	80
85	98	63
95	101	Pressure rising
105	100	
105	101	„ „ rapidly
120	101	„ „ „
135	104	113
Arteries released	..	Pressure falling rapidly
145	112	
155	120	89, lowest pressure
165	124	
170	126	Fall ceases and rise begins

NOTE.—The fall is the same on liberating the arteries if no nitrite has been previously given.

In FILEHNE'S second experiment, whilst giving nitrite by inhalation he circulated normal blood through a Rabbit's ear in which there was entire vascular isolation. In view of the variations in the diameter of the auricular vessels of the Rabbit which may occur spontaneously, and even independently of the existence of a normal connection with the central nervous system, and further, because variation might easily arise from the strength of the electrical current which FILEHNE proposed to substitute for the normal nervous impulse, results drawn from such an experiment can scarcely be regarded as conclusive.

Another method of procedure was therefore adopted by us, consisting in the rapid and temporary ligation of all arteries passing to the head, and the injection of salt solution containing a certain amount of one of the nitrites through the cranial end of the carotid artery, one of the jugular veins having been opened on the cranial side of a ligature to permit escape of blood, and so hinder the production of a possibly abnormal intravascular tension in the brain.

In all cases the nitrite to the extent of $\frac{1}{38}$ cub. centim. was dissolved in 2 cub. centims. of ·7 per cent. salt solution. It must be premised that nitrite of amyl introduced by direct injection into the general circulation, causes a fall of blood-pressure.

The invariable result was that the blood-pressure rose instead of falling, and the characteristic fall of pressure did not occur until the clamps were removed.

A single experiment selected from a large number will serve to illustrate this point.

Experiment B.—A large cat was completely anæsthetised by ether. The arteries were prepared for experiment by connecting the right carotid with the manometer, resecting the ribs and the upper part of the sternum, ligaturing the right vertebral and placing on threads the left carotid and subclavian arteries, as well as the veins passing from the head on the same side. Artificial respiration was steadily maintained. The vagi were undivided.

Time.	Pulse.	Pressure.
secs.	In 1 minute.	In millims. Hg.
0 Before ligation or injection	108	86
18 Clamped left subclavian and veins, the jugular being opened on the cephalic side of a permanent ligature		
23	110	
28	112	
33	109	96
36 Left carotid ligatured	110	96
44 51 $\frac{1}{32}$ cub. centim. (= 0·0275 grm.; NO_2 = 0·0108 grm.) in 2 cub. centims. salt solution injected into carotid artery		
56	105	Rising rapidly
61	102	
66	104	
71	102	120
91	99	Slight fall
96	100	104
101	100	
Clamps removed		
106	106	Falling
111	108	„
116	110	„
131	115	74
141	109	84

There was no indication of any nitrite effect so long as the vessels were ligatured, although the nitrite must have passed to the medulla oblongata by vascular anastomosis, and so reached the chief vaso-motor centre. The subsequent injection of Berlin blue proved the access to the medulla in that manner.

There was a rise of pressure and slowing of the pulse from vaso-motor and vagus stimulation, as seen in the previous experiment.

The acceleration of the heart does not occur until after the ligatures are removed, the vagus inhibitory centre having been stimulated by the vascular stagnation up to this time; the stimulation of the inhibitory centre ceases on removal of the clamps, and cardiac acceleration follows in due course.

The above results, which have been repeatedly obtained, agree very closely with those of MAYER and FRIEDRICH, who found that, after all vessels passing to the brain had been ligatured for a considerable time, a fall of pressure still followed inhalation of the nitrite of amyl, and that when it had access only to the vessels of the brain no fall of pressure ensued.

Although these experiments are justified in their bearing on the question so far as it applies to the chief vaso-motor centre, *i.e.*, that situated in the medulla, it is necessary to bear in mind that additional vaso-motor centres probably exist in the cord, and upon them the nitrites might exert an influence independent of an effect on the peripheral vessels.

No perfectly satisfactory plan of eliminating these centres is in our hands, nor is there likely to be, unless a more exact localization of their position becomes an accomplished fact. We know from the researches of GOLTZ, SCHLESINGER, VULPIAN, LISTER, and others that stimulation of a sensory nerve is capable of causing a reflex constriction of arteries after section of the cervical cord has removed the influence of centres in and above the medulla oblongata.

But it is everywhere assumed that such centres are subordinate in their function to the chief centre, and amenable to the same influences, and if we accept this, and at the same time show that the chief centre gives no evidence of paralysis when the nitrite reaches it, it would be scarcely reasonable to suppose that subordinate centres are materially affected by it. There is, however, a further positive argument for the peripheral action of the nitrites upon the vessels, derivable from the effect which may be produced by them upon the blood-pressure after division of the splanchnics. This will be dealt with in a subsequent section.

Usual Modification of Pulse and Pressure on Nitrite Inhalation.

The phases in any inhalation of nitrite as regards the effect upon the blood-pressure may for purposes of comparison be divided into three:—

1. Blood-pressure unaffected.
2. ,, ,, falling and remaining at lowest point.
3. ,, ,, rising.

The effect on the pulse does not permit of so satisfactory a division. Frequently during the first two periods the pulse may show no alteration, but in the first half of the second period retardation may often be recognized, and this may give place to an acceleration towards its close. During the third period an acceleration usually takes place, but it will be shown that the rise of pressure may occur without acceleration, and may even be attended by retardation of the pulse.

The length of time that elapses before the fall of pressure commences varies slightly according to the phase of respiration at which the administration begins, *i.e.*, whether inspiration or expiration is in progress; but if the administration commences during inspiration—and with a little care it may usually be made to do so—the variation is very slight. The first fall is usually discernible in 4·5 to 5 seconds after the commencement of inhalation, and is not preceded by any rise of pressure. The fall of pressure progresses from this point till the maximum is reached. Suppose $\frac{1}{38}$ cub. centim. of the pure α-amyl nitrite is administered for the first time to a cat—the breathing being normally active,—the fall commences in 4·5 seconds and proceeds most rapidly during the ensuing 10 seconds, in which time it amounts to from 60 to

65 per cent. of the total reduction of pressure. After this point for the next 10 seconds the fall amounting to from 20 to 30 per cent. still continues, the lowest point after a further fall being reached on an average 35 to 40 seconds after the inhalation commenced. During the time subsequent to the 20 seconds of chief reduction the fall is necessarily very slight. There is considerable uniformity in the relationship of the various phases of the fall even when the total extent differs. This will be illustrated by the contrasted experiments α and β in the appended table.

FALL of Pressure.

Experimental dose.	Total in millims.	Began.	Per cent. in 1st 10″ after fall began.	Per cent. in 2nd 10″.	Per cent. in 3rd 10″.	Per cent. after lapse of 30″.	Time of greatest fall.
α { $\frac{1}{100}$ cub. centim. = 0·0088 grm.; NO_2=0·00346 grm.	25	5″	65·2	30·4	4·4	..	″ 33
β { 1st administration, $\frac{1}{42}$ cub. centim. =0·0209 grm.; NO_2=0·0823 grm.	44	5′	64	24	12	..	35
β_2 9th ” ” ”	35	5·5′	52·3	30	17·7	..	34
γ ” ” ”	35	5·5′	19·5	38·4	38·4	3·7	50

After repeated administrations of nitrite there is a tendency in most cases to a relative increase in the percentage of the second and third stages at the expense of the first (Exp. β and β_2 in table). Exceptionally, however, even when small doses such as the $\frac{1}{100}$ cub. centim. have been employed, no such deterioration is discernible.

In cases of repeated administration in which the extent of the fall has become reduced, the latency of the fall appears to be longer.

In such exceptional cases as that recorded (γ of the table), in which the minimal pressure is not reached for 45 to 50 seconds, the earlier part of the fall is retarded relatively to the later, and there is a tendency for the minimal pressure to be maintained for some 10 to 15 seconds, and for the succeeding rise to be slow.

The pressure is, however, in only a very small proportion of cases, long maintained at its lowest, even when the return to or towards the normal is slow. A slight upward tendency is recorded within a comparatively few seconds of the time at which the minimum was reached.

In the first administration of amyl nitrite this maintenance of minimal depression is particularly short; it is, in fact, no sooner touched than in from 5 to 8 seconds the rise commences. A more prolonged depression at the lowest point, or within two or three millims. of it, is observable when the nitrite has been given repeatedly, and this is especially the case when the administrations succeed one another rapidly. This point and the relatively long depression at or about the minimum will be referred to later on.

The rise of pressure may vary in speed even when the dose of nitrite remains equal. Amongst the circumstances which favour a rapid rise are—

1. The absence from the blood of any considerable amount of nitrite or possibly of the products of its decomposition. Hence the return is more rapid when few administrations have been made, and when a considerable interval has elapsed between the inhalations sufficient to admit of full excretion and the return of the blood to the normal.

2. From what has already been said regarding the power of vaso-motor influence to modify the nitrite effect, it follows that respiration may produce a strong effect by itself modifying the composition of the blood, and so indirectly stimulating, or to some extent weakening, the vaso-motor apparatus, central or peripheral. We do not deny that the activity of such centres may favour a reinstatement of tonus after an action upon the arterioles has produced a fall of pressure.

The respiration is itself considerably affected by nitrite of amyl, which first causes a slight slowing, succeeded by an acceleration of the breathing, amounting to from five to nine, and occasionally to twelve, respirations per minute. If, however, the administration is repeated several times without any long pause intervening, a very distinct slowing occurs. If the course of recovery of the blood-pressure is watched during these changes in respiration, it will be noticed that rapid recovery occurs, as a rule, during the acceleration of the respiration; but that after a distinct slowing has become established the rise is much more gradual. In the first condition the nitrite elimination is accelerated, and further the tonus of the arterioles is rapidly reinstated by the action of more highly oxygenated blood.

In the latter condition the respiratory centre is apparently not the only mechanism involved, as it has been noticed that the reduction in number of respirations, and the alteration in the relationship of expiration and inspiration, was very similar to the effect produced by division of both vagi, although in the latter case the breathing was somewhat deeper. Further, when this slowing effect has been produced, the vagi being intact, the respiration under the subsequent action of the nitrite after vagotomy was very much less affected than before vagotomy. There is an indication here of an action upon the terminations of the vagus in the lung, which KNOLL[*] has shown to be affected by many volatile substances. After frequently repeated administrations of doses of the $\frac{1}{30}$ cub. centim. of the nitrite, even if the pause between the administrations is sufficient for complete recovery of blood-pressure, the activity of the respiration centre is undoubtedly impaired. This effect occurs not only temporarily during inspiration of the nitrite of amyl, but as a more permanent condition, necessitating artificial respiration in order to prolong the life of the animal. At this time, however, when the activity of the respiratory centre has been so far reduced, it is easily demonstrated that if artificial respiration be suspended after the nitrite fall, the blood-pressure may frequently be recovered with great rapidity without any cardiac acceleration. With the much smaller doses employed in many of the experiments no such effect was produced upon respiration.

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[*] KNOLL, 'Sitzungsbericht d. Wiener Akad., Math.-Naturw.,' vol. 68, Part 3, p. 245.

The respiration is, however, only to be considered as an indirect agency in modifying the blood-pressure. The direct causes now present themselves for consideration.

A. Acceleration of the pulse.
B. Normal return of tonus in the arterioles.

A. The acceleration of the pulse has been regarded as the chief cause of the restitution of the blood-pressure. GUTHRIE, in 1859, pointed out the occurrence of acceleration. There is no doubt that acceleration usually accompanies the return of the pressure. PICK stated that large doses cause retardation of the heart from direct action upon its muscular substance. FILEHNE and others have observed that the Frog's heart is not accelerated, but rather retarded by the nitrite. We have observed the same result with *Rana temporaria*, both from hypodermic administration to brainless animals and from exposure of the heart to very dilute nitrite vapour.

The great variation in the amount of acceleration seems to have passed almost unnoticed hitherto. The curves obtained from FICK's manometer have been measured in a very large number of experiments; and we have obtained some information on this point. The curve under inspection was divided before, during, and after the administration of the nitrite into intervals of 5 seconds, and we then measured accurately the number of beats and fractions thereof occurring in each interval. The average increase (cat) in terms of 1 minute for doses of the $\frac{1}{38}$ to $\frac{1}{42}$ cub. centim. nitrite of amyl is thirteen to twenty beats, and the chief acceleration occurs in 40 to 45 seconds after inhalation begins. The average time of occurrence of greatest reduction of pressure is 32 to 35 seconds.

Exp. B.—Full grown cat. Steady etherisation. Had received 20 minutes before one dose of pure amyl nitrite. Vagi intact.

Time.	Pulse.	Pressure.	Respiration.
secs.	Per 1 minute.	Millims.	
Before inhalation	160	139	25
0 Inhalation of $\frac{1}{50}$ cub.centim. pure nitrite of amyl = 0·0176 grm.; NO_3 = 0·0692			
5	159	139	
10	159	Falling	22·4
15	158		
20	160	. .	22·4
25	161		
30	161	104	18·4
35	162		
40	165	Rising	
45	174	. .	20
50	173		
55	168		
60		. .	23
70	166	. .	33
80			
90	164	139	

With much smaller doses than those just specified, say the $\frac{1}{100}$ cub. centim., α-amyl nitrite is still capable of causing an acceleration of pulse rate, though its extent is not so marked as after the larger dose.

The average is from 7 to 10 beats per minute. Thus, it appears that up to a certain point, acceleration is increased in proportion to the augmentation of the dose. Very large doses frequently retard the heart in all phases of their action. The time during which acceleration manifests itself may terminate abruptly at the 50th or 60th second. In either case it not unusually happens that the pulse becomes subnormal for a time. The pulse acceleration is often preceded by a distinct slowing (such an effect is observable in the experiment just quoted). This may appear 5 seconds after inhalation has commenced, and may continue 10 seconds, or occasionally for 20 seconds. The extent of this retardation is up to, but seldom beyond, the proportion of 4 beats per minute. After section of the vagi this retardation disappears, and it seems probable, therefore, that it is to be regarded as a reflex phenomenon to which the intact vagal apparatus is necessary. This effect is probably due less to an absorption of inhaled nitrite and resulting action on the vagus centre, than to a local effect on the peripheral vagi in the pulmonary tissues; it cannot be laryngeal, as the animal breathed by a tracheal cannula.

If this surmise is well founded, the vagi play the part of both afferent and efferent nerves in this reflex action.

To return to the subsequent acceleration of the heart, the following variations in the relationship of pressure and pulse have been not unfrequently observed; they may be taken as types of the more usual exceptions. An example of each will be recorded. They are taken from all stages of experiments, and, therefore, the variations in blood-pressure reaction are considerable.

(1.) An acceleration of the pulse amounting to 5–7 beats at the end of 20 seconds inhalation, lasting for 20 seconds only, and disappearing altogether before the rise of pressure has been well established.

Experiment XII., 10.—Gave $\frac{1}{48}$ cub. centim. (= 0183·0 grm.; NO_2 = 0·0072 grm.) pure α-amyl nitrite. Pressure fell from 91 to 65 millims. In 116 seconds rose to 84 but remained subnormal for 3 minutes. (Pulse accelerated 5 at end of 20 seconds, and in 40 seconds has regained the normal.)

(2.) The pressure remaining subnormal for a considerable time, followed by a slight pulse acceleration, appearing late, and disappearing before the pressure had regained the maximum.

Experiment.—Gave $\frac{1}{38}$ cub. centim. pure nitrite of amyl. Pressure fell from 96 to 70 millims. (Pulse retarded during inhalation, and only accelerated at rate of 2 beats per 1 minute 80 seconds after its termination. Thereafter slightly slowed again.)

In 1 minute recovered to 84.
„ 2 minutes „ 87.
„ 4 „ „ 97.

(3.) No acceleration of the pulse occurring, but the pressure rising to its original level within 2 to 3 minutes.

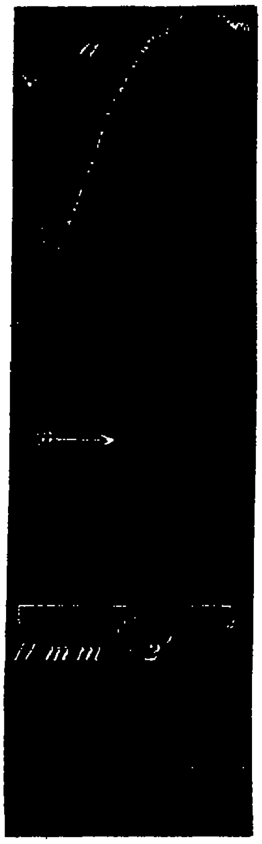
Experiment.—Gave $\frac{1}{38}$ cub. centim. pure nitrite of amyl. Pressure fell from 151 to 108. No acceleration of the pulse occurred throughout.

In 1 minute was 133 millims.
„ 2 minutes „ 150 „
„ 3 „ „ 154 „

(4.) An actual slowing of the pulse throughout (rare with nitrite of amyl for the doses examined).

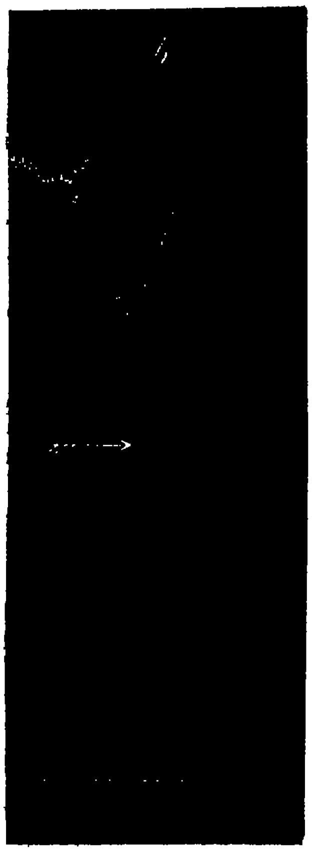
The Pulse after Vagotomy.—If it were granted that the acceleration of the pulse after nitrite of amyl is owing only to a lowered tonus of the vagus centre, as has been supposed by **Filehne** and **Pick**, we should reasonably expect that, after both vagi had been divided, inhalation would not be followed by acceleration, and we might further anticipate that if the rise of blood pressure were only due to pulse acceleration, a very prolonged depression would necessarily follow the section. **Filehne** cut the vagi of a rabbit, and obtained—unusual in the case of such an animal—an acceleration of over 20 beats per minute. After stimulating the peripheral portion of the vagi, so as to reduce the number of heart beats to the normal, he (F.) gave nitrite by inhalation till convulsions occurred, and found that although the vessels of the ear dilated, there was no further acceleration.

Tracing 1*a*.



Inhalation of $\frac{1}{42}$ cub. centim. α-amyl nitrite before vagotomy.

Tracing 1*b*.



Inhalation of $\frac{1}{42}$ cub. centim. α-amyl nitrite after vagotomy.

Whilst admitting that the usual amount of acceleration is not attained after vagotomy, it must still be insisted that a slight acceleration is usually to be observed. This acceleration, which may not amount to more than 15 to 20 per cent. of the previous amount, usually has its maximum 30 seconds after the inhalation is begun, and lasts for a shorter time than it does when the vagi are intact.

In one experiment the regularity of the acceleration produced by amyl nitrite was greater after than before vagotomy, though in amount it fell far short of the greatest acceleration with the vagi intact. The following figures may serve to give some idea of the nitrite effect in the same animal before and after vagotomy respectively. (XII., 18.) (See tracings 1*a* and 1*b*.)*

	Before section of vagi.	After section of vagi.
	millims.	millims.
Fall of pressure . .	35	33·5
Rise to normal in . .	109	120
Pulse before . . .	162	166
Respiration	25	19

Commenced inhalation of $\frac{1}{42}$ cub. centim. A. N. (= 0·0209 grm., NO_2 = 0·00823 grm.).

Time.	Pulse.	Respiration.	Pulse.	Respiration.
seconds.				
0				
5	159			
10	159	22·4	166	19
15	157			
20	159	22·3	166	
25	159	22·4		
35	161		171	Steady
40	169	18·4	171	"
50	175	20	170	"
60	168		170	"
70	166	23	166	"
80	168	23		
120	162			

One is therefore brought to the conclusion that small doses of pure α-amyl nitrite may accelerate the heart by directly stimulating it.

---

* The figures taken upon the slowly-moving cylinder from a mercurial manometer show changes in blood-pressure only. The movements of the pulse rate are taken from the rapid tracing of the FICK'S kymograph. The latter are given as figures when of sufficient importance. Where both manometers are open at the same time the form of the pulse is not accurately recorded, but its rate is reliable.

Rise of Pressure from Return of Tonus in Arterioles.

Attention has already been drawn to the fact that recovery of pressure, after small doses of pure nitrite of amyl, may occur without any direct pulse acceleration. Since no evidence of increase in the amount of blood discharged from the heart at each contraction is derivable from a study of the pulse, the return of contraction to the arterioles which had been dilated by the nitrite must be regarded as the cause of the rise. The instances (observed in cats) in which a fall of pressure was followed by a return to the normal without the occurrence of acceleration, are not those alone in which the original fall is insignificant; on the contrary this phenomenon is often observed during the earlier administrations of the nitrite in which the fall is so great as to amount to from 30 to 44 per cent. of the total pressure.

On looking over a large number of experiments (on cats) it appears that administration of from $\frac{1}{32}$ to $\frac{1}{48}$ cub. centim. of nitrite is followed, in about 27 per cent. of cases, by one of the three following conditions, (1) by a slight slowing of the pulse in 2 per cent., (2) by no alteration, (3) by an increase of one or two beats per minute. In the remaining 73 per cent. there is a marked acceleration. In cases of this exceptional nature the return of pressure is not of uniform speed, it is more rapid before the administration of nitrite has been repeated, that is to say, before a lasting impression has been produced which tends to a deterioration of the tonus of the arterioles, favouring a gradual decline in maximal blood pressure. The return of pressure was not more rapid than when (with the same animal) a distinct acceleration of the heart occurred. Companion cases of acceleration and non-acceleration, taken from the same experiments, will be placed here side by side.

	Administration.	Fall.	Recovery.	Acceleration.
	cub. centim.	millims.	′ ″	
Exp. F. . .	$\frac{1}{50}$	26	3 3	none
	$\frac{1}{50}$	32	1 6	20 per min.
Exp. A. . .	$\frac{1}{32}$	43	2 40	none
	$\frac{1}{32}$	44	2 33	15 per min.

If administration of the nitrite is made during the spontaneous occurrence of Traube-Hering curves, the pressure is very rapidly recovered. The increased activity of the vaso-motor centre, as evidenced by these curves, is as insufficient to prevent the fall of blood-pressure after nitrite administration, as we know splanchnic stimulation to be, but it appears to shorten the nitrite effect somewhat as in the case of splanchnic stimulation, causing a rise of pressure to the normal, with a quite unusual rapidity.

Intra-Vascular Injections of α-Amyl Nitrite.

The solutions for injections were made by introducing small measured quantities of α-amyl nitrite into the barrel of a hypodermic syringe, into which 2 or 5 cub. centims. of neutral or very slightly alkaline salt solution had been previously drawn.

The syringe was closed, shaken, and immediately fitted into the india-rubber continuation of the cannula, which had been previously introduced into the cranial end of the carotid artery, or into the central end of the saphenous vein respectively. The cannula was closed until the time for injection had arrived, when the clamp was removed and the contents of the syringe slowly expelled into the vein. The syringe was again partly filled with 2 cub. centims. saline solution and discharged into the cannula, thus driving all the nitrite solution into the circulation. The injection was made in all cases with a rapidity as nearly equal as possible. Administration of the nitrite by inhalation was made both before and after the injections for the purpose of contrast.

Intra-venous injections may be attended by a slight and transitory rise of blood pressure, amounting to from 2 to 4 millims., or this rise may be absent. A rapid fall occurs after this rise, or, in its absence, shortly after administration. A partial recovery of pressure succeeds the fall with tolerable rapidity, and this may progress steadily, or be soon arrested, the blood-pressure in the latter case returning gradually towards the normal. During the return a secondary fall is not unfrequent.

Intra-arterial injection delivered into the carotid towards the head is always attended by an initial rise, then by a more gradual fall than is shown after intra-venous injections, the point of minimal pressure being reached later, though the total fall is never so extensive.

Recovery at first rapid, usually shows a secondary fall, and then a gradual rise towards the normal.

An experiment will be quoted in which there was

α.—Administration of $\frac{1}{38}$ cub. centim. by inhalation.
β.—Administration of $\frac{1}{38}$ cub. centim. by intra-venous injection.
γ.—Administration of $\frac{1}{38}$ cub. centim. by intra-arterial injection.

The alteration of pulse as well as of pressure will be recorded in these cases.

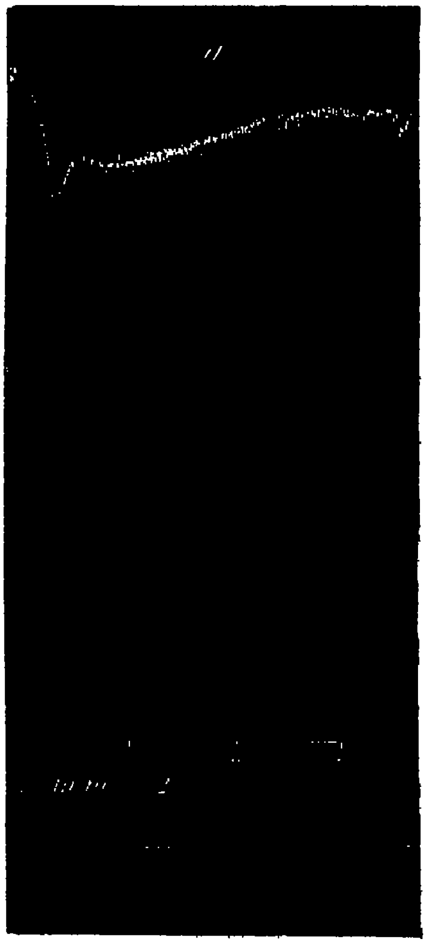
Exp.—Cat of large size. Cannulas in trachea, in the distal end of the left carotid for injection, and in the proximal end for manometer, also in saphenous vein. Steady etherisation.

A. Injection of $\frac{1}{38}$ cub. centim. of amyl nitrite dissolved in 5 cub. centims. salt solution into central end of saphenous vein. Pressure fell from 142 to 108 = 34 millims.

In 2 minutes the pressure was 113 millims.
„ 4 „ „ „ „ 118 „
„ 6 „ „ „ „ 120 „
„ 10 „ „ „ „ 148 „

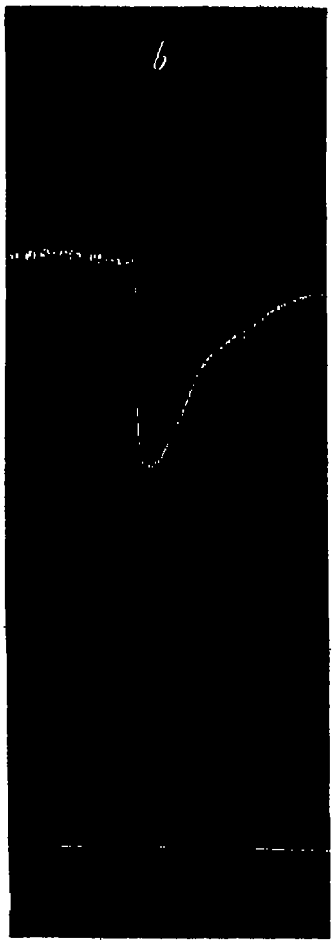
	Time. secs.	Pulse.	Respiration.	
Before injection . . .	..	180	46	
During injection . . .	5	180		
	10	176	45·5	
	15	177	..	Pressure began to fall.
	20	174	45·5	
After injection . . .	5	176		
	15	177	50	
	20	..	..	Rapid fall began.
	25	177	48	
	40	185	48·5	Pressure at lowest.
	60	185	57·5	
	80	182	55	

Tracing 2*a*.



Injection by carotid artery of $\frac{1}{38}$ cub. centim. α-amyl nitrite.

Tracing 2*b*.



Inhalation of $\frac{1}{38}$ cub. centim. α-amyl nitrite.

Injection of $\frac{1}{38}$ cub. centim. of amyl nitrite in 2 cub. centims. salt solution into cranial end of *carotid.*

Original pressure 153, rose 3 millims. and then fell to 126 = 27 millims.

Fall commenced 22 seconds after injection was begun.

In 2 minutes the pressure was 133 millims.
„ 4 „ „ „ „ 139 „
„ 6 „ „ „ „ 144 „
„ 8 „ „ „ „ 145 „

	Time.	Pulse.	Respiration.	
	secs.			
Before injection . . .	..	144	40	
During injection of $\frac{1}{38}$ cub. centim. amyl nitrite.	5	145		
	10	146	38·5	
	15	145		
	20	138	36	Injection finished.
Tracing 2a.	35	143	38·5	
	40	..	..	Rapid fall of pressure began.
	45	146	40	
	55	146	39·5	
	60	145	39·5	
	90	145	40	
	100	141	38·5	
	120	137	40	

After two more injections had been made, a marked deterioration of the blood-pressure was produced. At this time (40 minutes after the injection just described) an inhalation was given of $\frac{1}{38}$ cub. centim. of pure nitrite of amyl, with the following results.

Blood-pressure fell from 114 to 75 millims. Tracing 2b.

Fall commenced in 55 seconds.
In 2 minutes pressure was 101·5.
„ 3 minutes 50 seconds pressure was 110.

	Time.	Pulse.	Respiration.
	secs.		
Before inhalation	..	141	40
During inhalation lasting	20	140	41
After inhalation	20	146	44
	35	154	46
	55	157	45
	70	150	42
	85	148	40
	95	144	38

It has been found that this relationship of the effects produced by α-amyl nitrite are very constant according to the mode of administration.

The greatest total reduction of pressure is produced by inhalation; but this is the least prolonged in its action. The minimal pressure is recorded sooner after inhalation. The fall of pressure after intra-venous injection is greater than that following intra-arterial injection. After the latter the initial rise is always more marked than after the former.

Pulse acceleration is greater after inhalation than after intra-venous injection, and is least in intra-arterial injection. This relationship will be compared with that obtained on injection of iso-butyl nitrite, primary propyl nitrite, and ethyl nitrite respectively. It will be shown that the series which may be formed, according to the activity of the various nitrites in reducing blood-pressure, is not identical for administration by inhalation and intra-venous injection respectively.

Intra-venous injection of $\frac{1}{100}$ cub. centim. of α-amyl nitrite produces a marked reduction of pressure with pulse acceleration.

IV.—The Action of other Paraffinic Nitrites contrasted with that of Amyl Nitrite.

The number of experiments which have been requisite to afford a contrast of the following nitrites one with another has necessarily been large; for it was evident from the first that the only reliable means of comparison was to be obtained by administering certain of them to the same animal under conditions as nearly similar as possible. Several repetitions of each experiment were necessary for confirmation.

We have already mentioned some of the directions in which special precautions were taken, such as :—

(1.) The administration of equal quantities by volume of the nitrites, as estimated by very delicate measurements.

(2.) The steady and uniform administration of ether.

(3.) The maintenance of the temperature of the animal by keeping it in a warm box.

It has been shown in what ways the ordinary effect of pure α-nitrite of amyl may undergo modifications, and these variations have been somewhat accentuated to show the difficulties which must attend the contrast of a number of bodies which may vary so largely in their action on individuals.

After limiting the series which had been accumulated for the purpose of contrast by rejecting experiments in which the results were in any way doubtful, and after filling up the gaps by subsequent experiment, where it seemed necessary, it became possible to establish certain distinctions between the action of the bodies examined.

The relative effect produced by the various nitrites administered to the same animal, under as nearly similar conditions as possible, has been the guide in arranging them in order of activity. Whilst this order is deduced from a very large number of experiments it will only be possible to give a few examples of the results. Within certain limits animals differ in the degree of reaction they manifest towards the nitrites, so that a large dose to one will be productive of no greater result than a medium dose to another. The comparison of the action in various experiments must be conducted cautiously, at least two compounds being employed in each. It will be shown that, whilst the total effect of any one nitrite may vary in different experiments, its variation runs parallel with those of other nitrites. Thus amyl nitrite may produce a greater fall of pressure in Experiment B than in A; the same result will be obtained with iso-butyl nitrite, only the effect in both experiments is proportionately greater than that of the amyl compound.

Pure α-amyl nitrite has been already somewhat fully dealt with, so that reference can be made to its action for the purpose of contrasting with it other nearly related bodies, which contain a certain amount of β-nitrite.

The bodies were the following:—

		Per cent.	Marked.
(1.)	Amyl nitrite containing α-nitrite,	95	I.
	,, ,, ,, β- ,,	5	
(2.)	,, ,, ,, α- ,,	88·6	II.
	,, ,, ,, β- ,,	11·4	
(3.)	,, ,, ,, α- ,,	84·6	III.
	,, ,, ,, β- ,,	15·4	

These bodies were closely contrasted with the pure α-amyl nitrite, with one another, and also with the other members of the series of nitrites in which bases other than amyl were present.

They show amongst themselves only small variations in their activity upon the blood-pressure and pulse of animals examined under similar circumstances.

From nine experiments which dealt wholly, or in part, with the contrasted action of these bodies, the following facts have become clear:—

(1.) That the blood-pressure is reduced to a somewhat greater extent by the pure α-nitrite than by the other three. This difference in reduction is at most but a slight one, the proportionate increase from pure α-amyl nitrite being only about 3 per cent. above the next in activity of the three mixed nitrites, and not over 6 per cent. above the weakest.

These three bodies appear to fall into the following series when their pressure-reducing action is contrasted:—(1.) Most active (2.) Intermediate, between 1 and 3. (3.) Least active.

On consulting the table furnishing the composition of these bodies, it becomes evident that, at one end of the scale in this series, the pure α-amyl nitrite must be placed as the most active member, whilst at the other end is the mixed body containing the largest proportion of β-nitrite. The other two mixed nitrites take an intermediate position.

It has been said already that the variation in the activity of these bodies upon blood-pressure is really very small, and it may be stated here that though the repetition of experiments made it evident that a difference did exist between them, such as has now been indicated, we were at first inclined to believe their action identical.

The action of the mixed amyl nitrite group may be summarised by stating that the fall of pressure, the duration of depression, the speed and manner of its recovery, are closely similar with the exception of the slight variation already referred to.

The fall of pressure induced by their action is not, however, the only criterion by which we can contrast nitrite effects. The influence on the pulse is another in which a variation may be sought. It is not evident that any wider distinction exists between the various amyl nitrites in this respect. They, as a group, cause a relatively considerable acceleration in the heart-beats, and their action in this respect contrasts with the group in which alkyls other than amyl are present.

It has been pointed out that, according to the mode of administration, whether by inhalation or intra-vascular injection, &c., the action of α-amyl nitrite varies. Only one other member of the mixtures of amyl nitrites was tested by injection, but it was found that the two compounds were identical in their manifestations, with the exception of a slightly greater effect of α-amyl nitrite on the blood-pressure.

Tertiary Amyl Nitrite.

Contrasted with α-amyl nitrite this body proved itself more active in reducing the blood-pressure, whether administered by inhalation or injection. Especially by the latter method its greater activity is observable in the relatively greater extent of the fall of pressure and its more gradual recovery. It is worthy of note that, while after inhalation of the tertiary amyl nitrite the pulse is usually accelerated at least two beats above the effect caused by the primary compound, the result after injection was the opposite, and this may have contributed to the difference observed in the speed of recovery of blood-pressure.

In a sub-series of ten of the nitrites which were administered at the same period (February and March, 1890), and the results produced by which are strictly comparable, it was found that the primary and tertiary amyl nitrites were the two most active bodies in causing acceleration, though they came only midway as regards their power of reducing blood-pressure.

The prolonged effect of the tertiary compound on injection is striking.

The average reduction of pressure after $\frac{1}{100}$ cub. centim., given either by inhalation or injection, appears to be from 26 millims. to 31 millims. The recovery of pressure is slower than in the case of the primary compound.

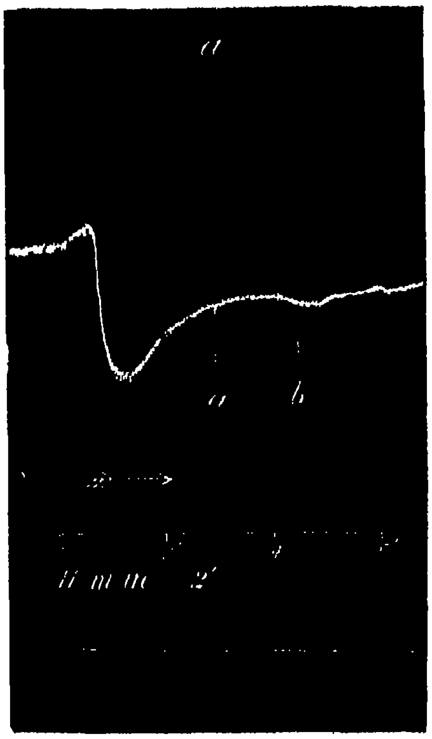
Tertiary amyl nitrite does not actively affect the respiration in the dose of $\frac{1}{50}$ cub. centim. (= 0·0178 grm.; NO_2 ·007 grm.) although it causes a slight slowing at first, occasionally followed by a faint acceleration.

The following figures will give an idea of the extent to which retardation in rise of blood-pressure may follow tertiary amyl nitrite inhalation.

Inhalation of Tertiary Amyl Nitrite.

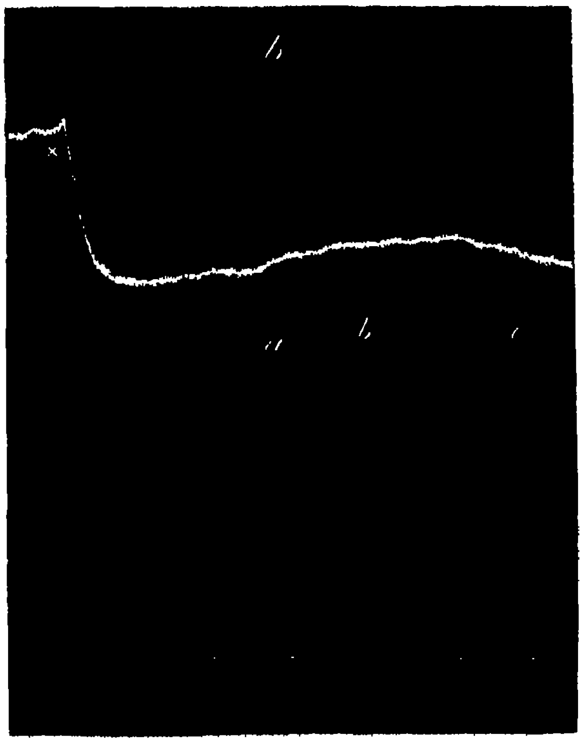
(25.3.90.) Cat of 5 lbs. Cannula in femoral vein. Breathing normally by the tracheal tube. Ordinary arrangement of apparatus. After tertiary amyl nitrite had been thrice administered by inhalation, $\frac{1}{100}$ cub. centim. (= 0·0089 grm.; NO_2 = 0·0035 grm.) was given. Tracing 3*a*.

Tracing 3*a*.



Inhalation of $\frac{1}{100}$ cub. centim. tertiary amyl nitrite.

Tracing 3*b*.



Injection by femoral vein of $\frac{1}{100}$ cub. centim. tertiary amyl nitrite.

The blood-pressure which at the commencement was 83 millims. fell in 40 seconds to 55 millims.

In 2 minutes the pressure was 69 millims.
„ 4 „ „ „ 70 „
„ 6 „ „ „ 74 „

The heart was accelerated at the rate of 14 beats per minute for 50 seconds, and the respiration 1 per minute.

Same animal. Injection of $\frac{1}{100}$ cub. centim. into circulation through femoral vein. Tracing 3*b*.

	Time.	Blood-pressure.	Pulse.	Respiration.
	secs.	millims.		
Before injection	0	107	146	43
$\frac{1}{100}$ cub. centim. tertiary amyl nitrite in 5 cub. centims. salt solution injected into femoral vein	5	. .	143	
	15	. .	144	42
	25	. .	144	
	35	. .	144	
	45	. .	146	40
	55	. .	149	
	65	76	155	41
	85	. .	155	
	95	. .	155	
	210	82	153	
	340	. .	120	42
	490	. .	118	43
	680	83		

The *butyl compounds* examined were the following :—

Normal (primary) butyl nitrite.
Iso-butyl nitrite.
Secondary butyl nitrite.
Tertiary „

Primary Butyl Nitrite.

Primary butyl nitrite will be first considered in this group; it stands physiologically somewhat removed from the other members.

It separates itself from iso-butyl nitrite by its comparatively feeble action, whether administered by inhalation or intra-vascular injection. Inhalations of doses of $\frac{1}{100}$ cub. centim. (= 0·0088 grm.; NO_2 = 0·00393 grm.) of butyl nitrite are followed by a prompt fall of pressure which varies in extent from 15 to 23 millims. The average fall observed in a large number of inhalations is 19 millims.

In average cases at the end of five minutes after the administration of such a dose the pressure is subnormal to the extent of 4 millims.

The speed of recovery of pressure cannot, however, be predicted with precision from the extent of the fall. A great fall may be succeeded by a prompt return to the normal within as short a time as 160 seconds, and on the other hand an insignificant fall may be maintained for a considerable time. In the former case the vaso-motor apparatus is active, and the vessels rapidly regain their tone; in the latter an opposite condition obtains; it is most commonly associated with the prevalence of a low pressure.

In small doses nitrite of butyl does not markedly accelerate the pulse. Taking the results of six inhalations from three distinct experiments, acceleration appeared in half the number, in two there was no alteration, and in one a slight retardation throughout. The average result of a large number of experiments in which $\frac{1}{100}$ cub. centim. was administered was found to be an acceleration of from four to five heart beats per minute. Such acceleration as may be produced is of rapid occurrence, and is frequently observed in 30 seconds after the commencement of inhalation. Respiration is retarded to the extent of four or five per minute after inhalations of $\frac{1}{100}$ cub. centim. butyl nitrite.

The contrast of butyl nitrite with amyl nitrite when given by inhalation shows the latter to be slightly more powerful in reducing pressure, somewhat more lasting in its effect, and more usually accompanied by acceleration. It has less effect upon respiration than the butyl compound.

Butyl nitrite when given by injection causes a more marked fall of pressure than when given by inhalation. When it is given by the former method the average fall is 23 millims., or about 17 per cent. more. In that case the fall is succeeded by even less acceleration of the pulse than when the nitrite is given by inhalation, from one to three beats per minute being the usual increase. The rise of pressure is slightly less rapid after the injection. Five minutes after the commencement there is still an average deficiency of from 5 to 8 millims.

(20.2.90.) Cat of 5 lbs. Steadily etherised. Administration of $\frac{1}{100}$ cub. centim. butyl nitrite in 5 cub. centims. salt solution by injection into femoral vein. The blood-pressure fell 22 millims. (124–102), and in five minutes was 115 millims. Tracing *4a*, *4b* (slow and quick drums).

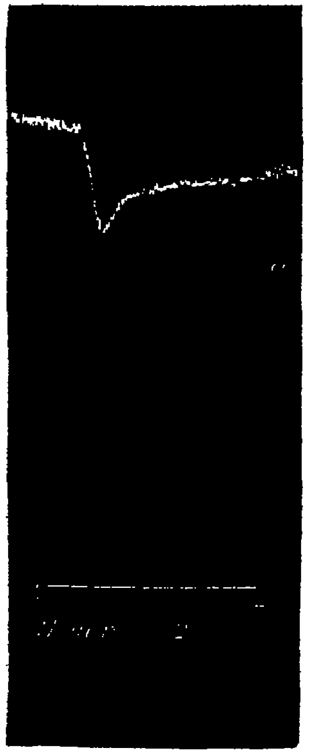
	Time. secs.	Pulse.
Before inhalation . .	..	133
During injection . .	0	130
	5	130
	15	132
	25	133
	40	133
	50	133
	70	132
	90	134
	110	132
	150	132
	240	138

Iso-butyl Nitrite.

This is one of the most active bodies examined in the whole series as regards the reduction of blood-pressure. Not only is this reduction of great extent, but it is produced with rapidity, so that the point of minimal pressure is soon reached.

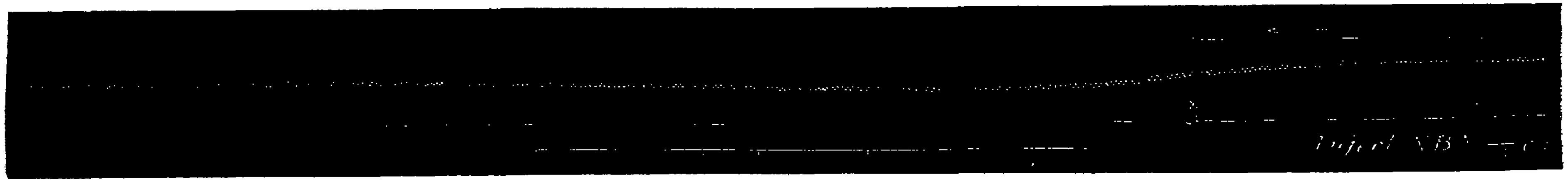
As in all the nitrites examined, the earliest administrations of the drug produce

Tracing 4*a*.



Injection by femoral vein of $\frac{1}{100}$ cub. centim. butyl nitrite. For changes in pulse see fig. 4^1.

Tracing 4*b*.



Injection by femoral vein of $\frac{1}{100}$ cub. centim. butyl nitrite in 5 cub. centims. salt solution. Reduced one-half. The upper tracing taken with Fick's kymograph, shows pulse and pressure; the lower, from a Marey's tambour, shows respiration, the point as in all experiments moving upwards on inspiration. For changes in pressure see record by mercurial manometer (4) on slow cylinder.

the above effects in the most marked degree. As the number of administrations is multiplied, a general deterioration in the blood-pressure becomes apparent, and the active nitrite fall is reduced in extent, though it still bears about the original relationship to the lower pressure which the greater fall did to the higher.

Under the progressive action of the drug, however, the return of pressure to or towards the normal is distinctly retarded, so that the time during which the pressure remains subnormal shows an increase with successive administrations.

The pulse rate is usually affected by inhalations of iso-butyl nitrite, but the modification it undergoes is not parallel with that which follows the action of pure α-amyl and tertiary amyl nitrites. In the earlier stages of its action—*i.e.*, subsequent to the first 15 seconds of administration of $\frac{1}{40}$ cub. centim. (= 0·0348 grm.; NO_2 = 0·0152 grm.)—an acceleration having the value of 4 to 5 beats per minute is witnessed, and this gives place to a further slight acceleration in the succeeding 20 or 25 seconds.

If the action of iso-butyl nitrite in this respect is contrasted with members of the amyl group, it becomes evident that the total acceleration produced by the former is by no means so marked as that produced by the latter, therefore the fall of pressure is not the only cause of acceleration.

The return of pressure to the normal is not dependent alone upon the pulse acceleration, as the pressure after iso-nitrite of butyl usually recovered more rapidly than after amyl nitrite, although the fall of pressure is much greater after the former, while the pulse acceleration is less.

From the rapid fall of pressure following the administration of iso-butyl nitrite, it is evident that a very prompt and complete vascular dilatation occurs.

This effect is not, however, of prolonged duration, the blood-pressure tends to rise rapidly, and often accompanied with a slight acceleration of the pulse; the returning tone of the vessels evidently playing an active part in this recovery.

The following experiment will serve to illustrate these points:—

Cat of 7 lbs. Steadily etherised from tracheal cannula. Vagi intact. Breathing natural. Tracings 5*a* and 5*b* (slow and quick cylinders).

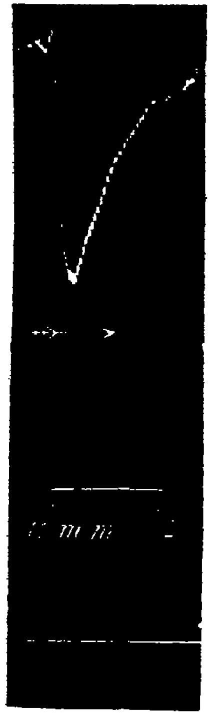
Administered iso-butyl nitrite by inhalation.

$\frac{1}{50}$ cub. centim. ($\doteq$ 0·0174 grm.; NO_2 = 0·0038 grm.).

Pressure rose 4 millims., and then fell.

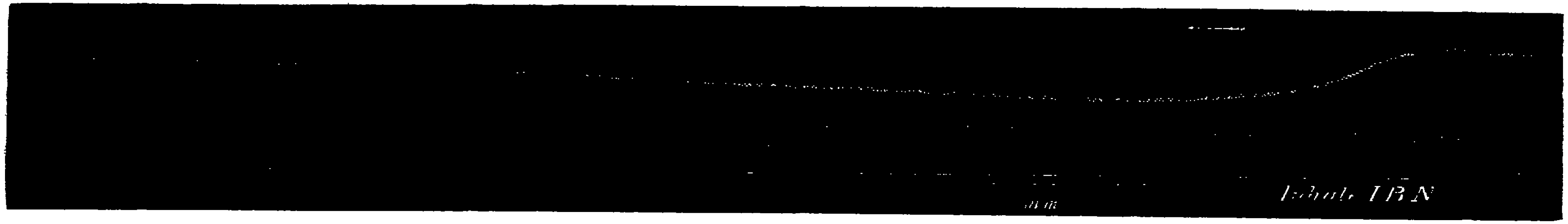
54 millims. (128–74 millims.). In 2 minutes it rose to 111; in 350 seconds to 117 millims.

Tracing 5*a*.



Inhalation of $\frac{1}{50}$ cub. centim. iso-butyl nitrite. (For pulse and respiratory tracings, see tracing 5*b*.)

Tracing 5*b*.



Inhalation of $\frac{1}{50}$ cub. centim. iso-butyl nitrite. Reduced one half. The upper line shows pulse and pressure, the second respiration, the lowest the signal marking time of administration. For pressure changes, see tracing 5*a*.

	Time.	Pulse.	Respiration.
	secs.		
	0	204	27
Admitted I.B.N.	5	204	
	10	205	27
	15	204	
	20	206	21·5
	25	204	
	30	206	20
	40	206	18·5
	50	200	13·5
	60	196	18
	70	196	17·5
	80	192	17
	90	192	16
	100	200	17
	105	204	17·5
	110	208	
	115	204	17
	125	..	17
	135	206	17
	180	..	22
	210	204	23

Before the administration the heart was accelerated, and the breathing was also rapid. The pulse showed a slight tendency to accelerate after the nitrite; the respiration on the other hand became slower, and remained subnormal for several minutes. Of course when the initial pulse rate is high, so large an acceleration is not to be expected as in cases when the initial rate is low.

Experiment.—Cat of $6\frac{1}{4}$ lbs. Usual preparation. Steady etherisation. Administration of $\frac{1}{48}$ cub. centim. (= 0·0182 grm.; NO_2 = 0·0079 grm.). The fall of pressure commenced 4 seconds after administration.

In 25 seconds it fell from 135 to 80 millims.
„ 90 „ pressure rose to 107 „
„ 110 „ „ 129 „

	Time.	Pulse.
	secs.	
Before nitrite	..	185
During „	15	182·5
	25	186
	30	186
	35	188
	45	190
	60	192
	75	192
	95	188
	115	180

With the result of this inhalation we can contrast one made with the mixed α and β-amyl nitrite (1) $\frac{1}{48}$ cub. centim. (= 0·018392 grm.; NO_2 = 0·00972 grm.).

Here the pressure fell from 121 to 77, or through 44 millims. The lowest pressure was reached in 30 seconds.

In 1 minute it had risen to 96.
„ 2 minutes „ „ 113.
„ 2 „ 54 seconds it had risen to the normal.

Greatest acceleration of the pulse amounted to 24 beats per minute.

Small doses.—Administration of such small doses as $\frac{1}{80}$ to $\frac{1}{100}$ cub. centim. of isobutyl nitrite by inhalation produces a marked fall in pressure, placing it much beyond the action of α-amyl nitrite and primary butyl nitrite.

The average reduction of pressure it induces in doses of $\frac{1}{100}$ cub. centim. is 45 to 50 millims., whilst the return of pressure is accompanied by an acceleration of the pulse rate averaging 4 to 7 per minute.

As to the duration of its action this appears to be somewhat shorter than after amyl nitrite, as the pressure is about normal in five minutes after the commencement of inhalation, whereas after amyl it is still subnormal at this time.

The bulk of the recovery, that is to say, from 70 to 75 per cent. of it, is in fact usually made in early inhalations, just within two minutes of the time when inhalation was commenced; the ascent after this shows a relative retardation which accounts for the total time occupied.

It is, however, no uncommon occurrence by a greater acceleration during the last stage for the pressure to regain the normal after a fall of 45 to 50 millims. in 3 minutes 30 seconds.

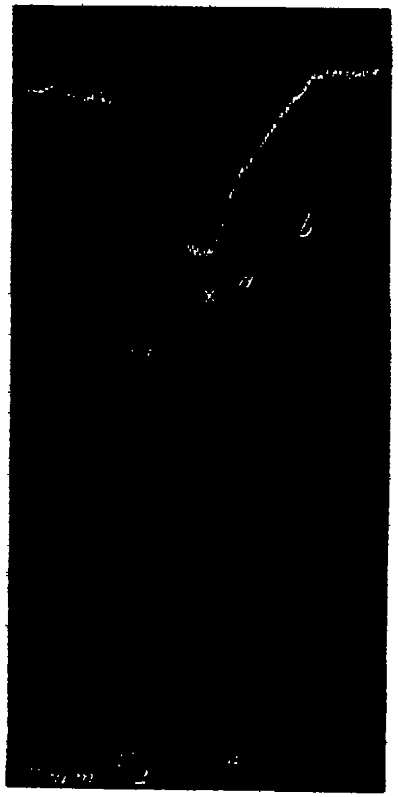
As with the larger dose so with the $\frac{1}{100}$ cub. centim. (= 0·0087 grm.; NO_2 = 0·0038 grm.), administered for the first few times, the breathing is greatly retarded, and even arrested for 20 or 30 seconds, but subsequently this tendency becomes less observable.

This effect, as well as the accelerated respiration which occasionally succeeds it, modifies the course of the blood-pressure.

Experiment G.—Tracing 6*a* and 6*b* (quick and slow cylinders). Cat of 6½ lbs. Cannula in carotid. Usual arrangement of apparatus. Normal amyl nitrite had already been given, but had not affected respiration.

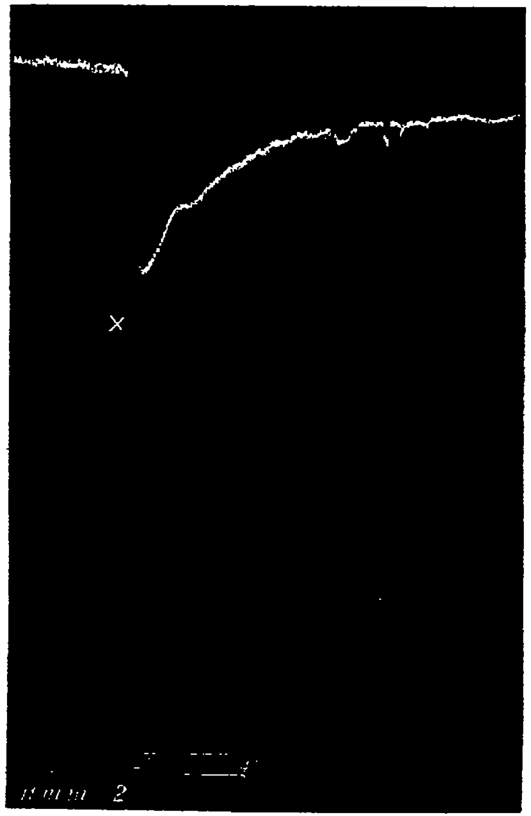
The blood-pressure fell 50 millims., and became normal again in 3 minutes 22 seconds.

Tracing 6*a*.



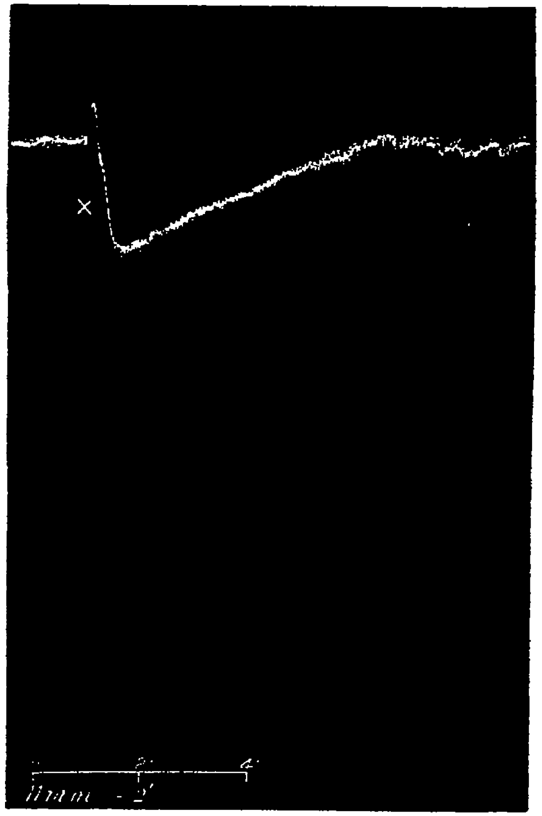
ıhalation of $\frac{1}{80}$ cub. centim. iso-butyl nitrite. The letters correspond with those in tracing 6*b* recorded on rapid cylinder.

Tracing 7*a*.



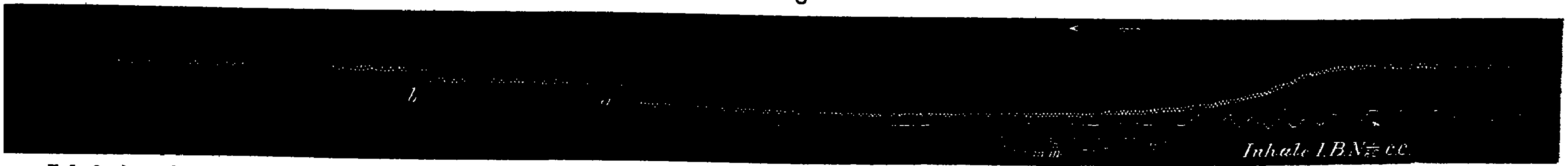
Injection by femoral vein of $\frac{1}{38}$ cub. centim. iso-butyl nitrite.

Tracing 7*b*.



Injection by carotid artery of $\frac{1}{38}$ cub. centim. iso-butyl nitrite.

Tracing 6*b*.



Inhalation of $\frac{1}{80}$ cub. centim. iso-butyl nitrite. Reduced one-half. The letters correspond with those in the corresponding slow record, tracing 6*a*. The upper line shows pulse; the lower, respiration. A star indicates the time of commencing administration.

	Time.	Pulse.	Respiration.
	secs.		
Before nitrite	. .	148	22
Inhaled $\frac{1}{80}$ cub. centim. iso-butyl nitrite	5	151	
	10	156	21
	15	159	
	20	162	21
	25	161	1
	30	158	
	35	156	
	40	. .	Stopped.
	45	154	
	60	152	
	65	. .	Recommenced.
	136	153	25
	210	156	25

Intra-vascular Administration of Iso-Butyl Nitrite.—The same small doses were used in these experiments which had been employed in inhalation.

The nitrite was discharged from the measuring pipette into salt solution previously introduced into the inverted barrel of a hypodermic syringe, which, after being well shaken, was fitted into the cannula.

The result differs according as the injection is made into the cranial end of the carotid artery, or into the central end of the saphenous vein.

27.5.90.—*Experiment.* After the *intra-arterial* injection in the experiment quoted, a comparatively slow fall was preceded by a distinct rise in pressure, the reduction of pressure was moderate (30 millims.), and its recovery fairly rapid (294 seconds). After the intra-venous injection, a much more abrupt and extensive fall of 45 millims. was preceded by only a slight rise of 5 millims., and the recovery of pressure, though at first more rapid, was ultimately slower; after 6 minutes it was still subnormal. Tracing 7*a*.

The period at which the fall begins likewise varied in the two cases.

After the venous injection the pressure fell below the initial pressure in 10 seconds, but after the carotid injection it fell in 16 seconds. In the former, the lowest pressure is reached in 37 seconds; while in the latter, it is reached in 52 seconds.

Changes in the pulse were as follows :—

	Time. secs.	Pulse.
Before injection	..	164
During 20 seconds injection of $\frac{1}{38}$ cub. centim. (= 0·0229 grm.; NO_2 = 0·08 grm.) iso-butyl nitrite by saphenous vein	..	164
After injection finished	5	165
	10	160
	15	158
After injection	20	157
	25	156
	30	155
	35	157
	40	158
	45	159
	55	159
	65	160
	85	160
	105	156
	125	157
	145	160
	185	167

Injection into carotid artery of $\frac{1}{38}$ cub. centim. 25 minutes after the injection just recorded. Tracing 7*b*.

	Time. secs.	Pulse.
Pulse before	..	156
During injection into carotid artery (30 seconds)	..	156
After	5	157
	10	150
	15	146
	20	145
	25	145
	30	145
	35	149
	40	151
	50	151
	75	152
	85	156
	100	156
	140	151
	175	156
	210	153

The absence of any acceleration during the first 3 minutes is marked, as is the presence of a positive retardation amounting to 9 beats per minute in the intra-saphenous injections, and to 11 beats in the intra-carotid.

Injection of small doses of Iso-Butyl Nitrite.—A dose of $\frac{1}{100}$ cub. centim. is more active in causing a fall of blood-pressure when administered by inhalation than by intravenous injection. The average fall it produces in the latter case is 34 millims. and the return of pressure to the normal is slightly later than in the case of inhalation. Under these conditions the pulse acceleration, if it occurs at all, amounts to not more than 4 per cent.

Localisation of action of Iso-Butyl Nitrite.—The series of experiments employed in determining the mode of action of α-amyl nitrite was repeated in the case of iso-butyl nitrite (p. 520, *et seq.*).

The general results obtained were similar, indicating a peripheral rather than a central effect. The tendency to an elevation of blood-pressure when the injection of the compound in solution was made toward the head, was a marked result, as was the fall of blood-pressure when administered by inhalation after all the vessels passing to the head had been temporarily ligatured.

Action of Iso-Butyl Nitrite on Respiration.—A marked retardation of respiration or even arrest in expiration is produced by this body. This result is well illustrated in tracing 6*a* (fast drum) in this tracing the retardation of respiration causes a check in the recovery of pressure; a subsequent rapid recovery occurring after the respiration is re-established. The serious and lasting interference with respiration which methyl nitrite occasions is not produced by the nitrite under consideration.

Secondary Butyl Nitrite.

This compound shares to a large extent the powerful properties of iso-butyl nitrite.

It causes a rapid and considerable fall in blood-pressure, followed by a recovery towards the normal which is usually rapid in its commencement, but tends to become slower as it approximates to the original level.

The fall is equal to, or slightly more considerable than, that of iso-butyl nitrite, and the recovery appears to be slower. An examination of the pulse rate shows a decided retardation during inhalation succeeded by a somewhat slowly developing acceleration. This acceleration is by no means an extensive one, and in this respect the drug appears to stand near the iso-butyl nitrite, and to differ from the amyl compound.

When so small a dose as the $\frac{1}{100}$ cub. centim. of secondary butyl nitrite is inhaled or injected, it produces a marked reduction in the blood-pressure.

The average fall after inhalation is 43 to 52 millims., and the recovery of pressure occurs slightly later than after either iso-butyl nitrite or tertiary butyl nitrite. The acceleration of the pulse is not extensive (frequently 5 to 7 per minute), as in the case of butyl nitrite. It may be absent altogether till late in the course of administration as illustrated by tracing 8. On respiration it has a powerful effect, causing a very marked retardation, frequently with a tendency to pause in inspiration.

The following experiment may illustrate the action of this body, though the effect is somewhat subnormal.

31.5.90.—*Experiment.* Cat (large). Steadily etherized by special apparatus. Vagi intact and breathing natural. Tracing 8.

1. Administration of $\frac{1}{100}$ cub. centim. (= 0·0087 grm.; NO_2 = 0·0038 grm.) of *secondary butyl nitrite.* Fall commenced in 4 seconds. Blood-pressure fell 43 millims. (115 to 72) its lowest point reached 32 seconds after inhalation commenced.

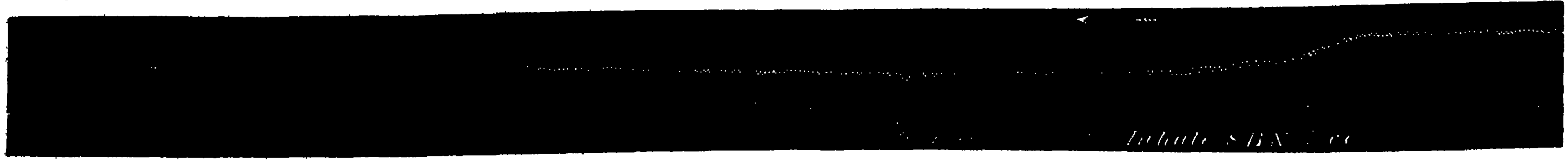
In 2 minutes blood-pressure rose to 100 millims.
„ 7 „ „ „ „ 112 „

	Time.	Pulse.	Respiration.
	secs.		
Before inhalation . . .	0	176	19·5
Inhalation commenced .	5	174	
	10	174	19·5
	15	173	
	20	172	Pause in position between expiration and inspiration
	30	168	
	40	172	
	50	174	12
	70	174	15
	80	174	17
	90	175	18
	100	181	18
	110	181	20
	120	184	19·5
	135	182	17·5
	150	180	17·5
	160	175	15
	230	170	15

Secondary butyl nitrite when injected ranks as one of the most active of the nitrites, but when thus administered its effect is less than after inhalation by some 5 to 6 millims. in the fall of pressure.

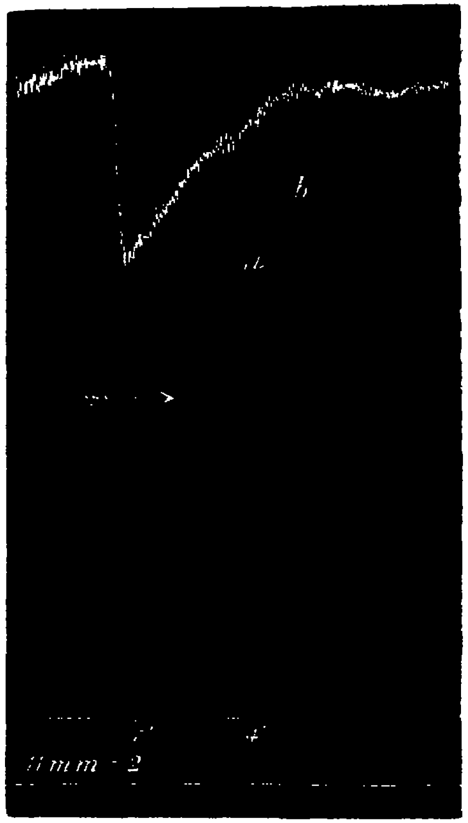
If the average fall after inhalation is 43 to 53 millims., after injection it is 40 to 45; while after injection, the return is comparatively rapid (average pressure is − 6 millims. in 5 minutes) in spite of the fact that acceleration is usually no more than 1 to 3 per minute. The fall after injection is slightly greater than after an equal dose of iso-butyl nitrite.

Tracing 8.



Inhalation of $\frac{1}{100}$ cub. centim. secondary butyl nitrite. Reduced one-half. The upper line shows pulse and pressure; the second, the respiration; the lowest, the signal giving time of administration.

Tracing 9.



Injection by femoral vein $\frac{1}{100}$ cub. centim. secondary butyl nitrite.

SECONDARY butyl nitrite.

31.5.90.—The pressure fell 41 millims. In 5 minutes was 7 millims. Tracing 9.

	Time.	Pulse.
	secs.	
Before	. .	133
Injection of $\frac{1}{100}$ cub. centim. secondary butyl nitrite by femoral vein	0	
	10	133
	15	128
	20	127
	30	134
	40	133
	50	132
	80	132
	100	133
	160	127

Tertiary Butyl Nitrite.

The compound now to be considered is one of the most active in the series in its effect upon blood-pressure. It acts like iso-butyl nitrite in reducing the pressure with great rapidity and power, doses so small as the $\frac{1}{32}$ to $\frac{1}{40}$ cub. centim.* usually causing a fall amounting to 40 per cent. of the entire blood-pressure, and even so small a dose as the $\frac{1}{100}$ cub. centim. produces a large reduction.

After the greater part of the fall has occurred rapidly the point of minimal pressure is somewhat gradually reached, and the rise then commences. Even in the earliest stage this rise is more gradual than that after iso-butyl nitrite; and as the phase develops, the relative retardation becomes even more apparent, the pressure remaining subnormal much longer. This effect is not attributable to cumulative action from frequent repetition of the nitrite dose, for it occurs in instances of first inhalations; nor does it take place merely as a part of a general peculiarity in individual reaction to the nitrites, as the iso-butyl nitrite or one of the amyl nitrites administered after it will be succeeded by a relatively rapid recovery to the original pressure. The early part of the action is clearly that of the butyl compounds; the latter part differs from them in the greater duration of the effect.

The earlier part of recovery of pressure is usually decidedly slower after this nitrite than after those just mentioned.

The pulse variation runs parallel at first with that of the iso-butyl nitrite; slight retardation is not unusual during inhalation, and some degree of acceleration may be noticed in from 20 to 30 seconds; this acceleration is usually 10 to 14 beats per minute (for the $\frac{1}{80}$ to $\frac{1}{40}$ cub. centim.), but after the lapse of 80 to 100 seconds a more marked acceleration makes its appearance, and may continue for several minutes.

---

* During one experiment the effect produced was very remarkable. The $\frac{1}{30}$ cub. centim. reduced the pressure on administration 106 millims.; a second inhalation reduced it from 150 to 20, respiration being completely paralysed, but recovery occurred after artificial respiration. Subsequently a fall of 70 millims. resulted from the administration of $\frac{1}{100}$ cub. centim. only.

The following figures are taken from an experiment in which the action of the butyl compounds was closely contrasted. Tracing 10*a* and 10*b*, quick and slow drums.

Cat of 4½ pounds; receiving ether steadily; breathing naturally. Administered $\frac{1}{80}$ cub. centim. (= 0·0107 grm.; NO_2 = 0·0046 grm.) tertiary butyl nitrite.

Fall commenced in 5 seconds.

Pressure fell 55 millims. in 55 seconds (118–63).

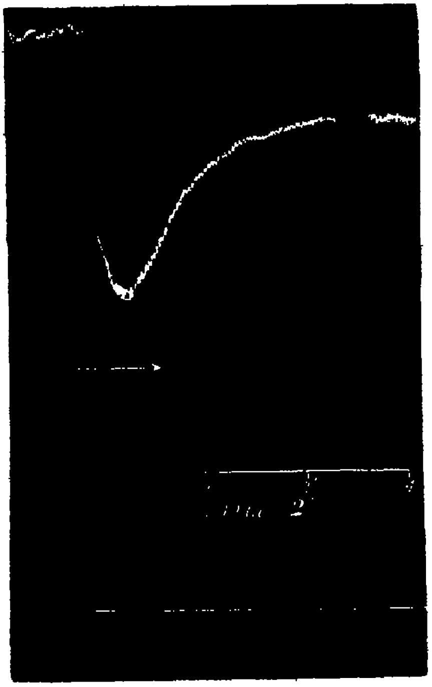
In 2 minutes rose to 90 millims.
„ 4 „ „ „ 98 „
„ 8 „ „ „ 103 „

	Time. secs.	Pulse.	Respiration.
Before inhalation . .	0	174	27
Commenced inhalation of tertiary butyl nitrite $\frac{1}{80}$ cub. centim.	5	168	
	10	172	Two respirations occur, passing gradually into partial inspiration at end of 20 seconds and of 55 seconds
	15	176	
	20	178	
	25	172	
	30	172	
	40	174	20
	50	180	20·5
	60	180	
	70	182	20
	80	186	20
	90	183	19·5
	100	180	19·5
	110	186	17
	130	184	15·5
	160	186	16
	200	186	16
	230	192	18·5
	266	198	19·5

The action which is produced in this experiment upon respiration is very marked; a prolonged pause is only broken by one faint expiratory effort during 35 seconds when respiration recommences.

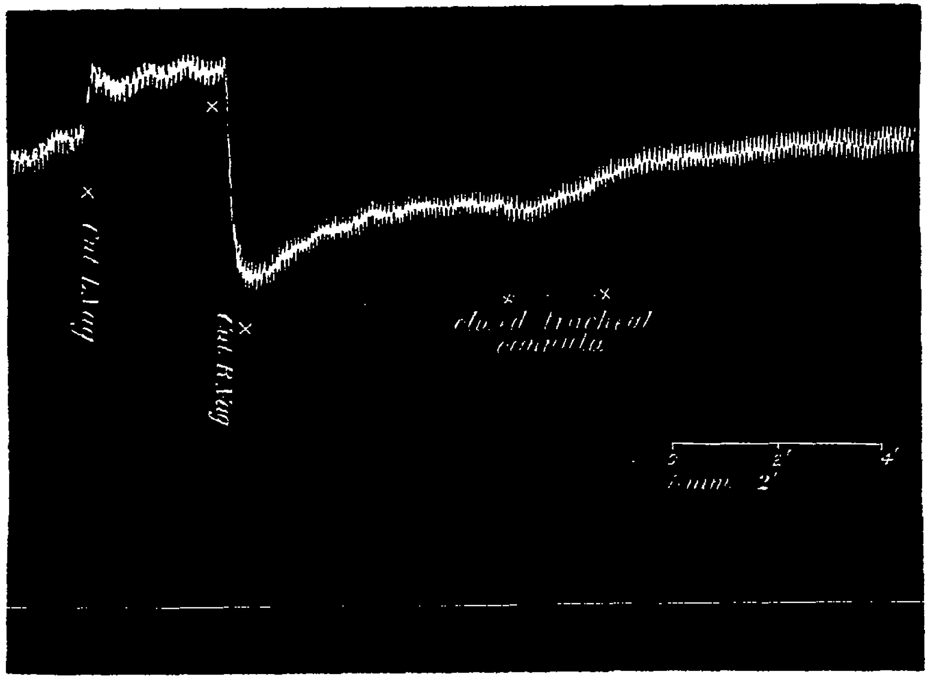
Section of Vagi. Tracing 11.—Section of vagi immediately after greatest reduction of pressure. After obtaining a reduction of the blood-pressure, very similar to that just described, $\frac{1}{100}$ cub. centim. tertiary butyl nitrite was administered, artificial respiration being carried on. The pulse, originally 144, fell to 141 during inhalation,

Tracing 10*a*.



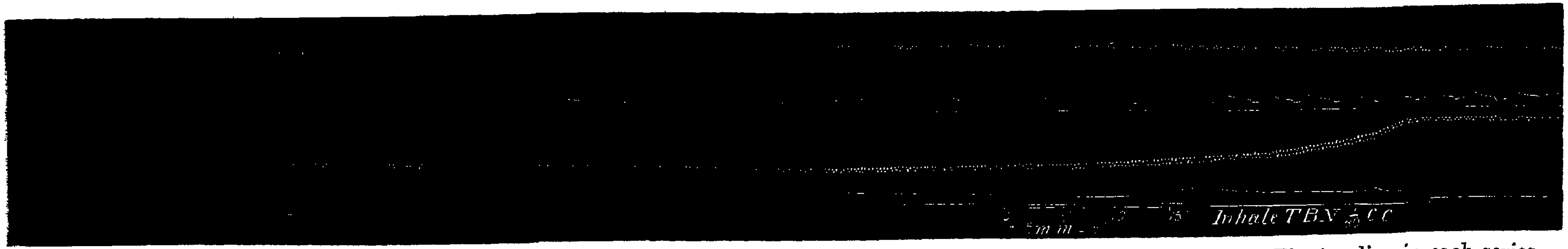
Inhalation of $\frac{1}{80}$ cub. centim. tertiary butyl nitrite. (For pulse and respiration, see quick tracing, 10*b*.)

Tracing 11.



Inhalation of $\frac{1}{100}$ cub. centim. tertiary butyl nitrite. Section of both vagi is made, that of the second being at the point of lowest pressure. The tracheal cannula is subsequently closed for 50 seconds.

Tracing 10*b*.



Inhalation of $\frac{1}{80}$ cub. centim. tertiary butyl nitrite. Reduced one-half. The upper series is continuous with the lower. The top line in each series shows pulse and pressure; the second, respiration; the lowest, the signal record of administration. See also pressure tracing (10*a*), taken on slow drum.

and then rose to the original number. The right vagus was then divided, the left having been already cut, but no acceleration in pulse-rate ensued, the number varying during the ensuing 5 minutes from 137 to 144. The pressure showed but little tendency to rise, though a considerable reduction in the calibre of the tracheal cannula produced some effect upon it.

The pressure varied as follows :—

Pressure 109 millims. fell to 67 millims. in 45 seconds.
30 seconds after commencing inhalation divided vagi.
2 minutes pressure 76 millims.
4 ,, ,, 81·5 millims.
6 ,, ,, 81 millims., partly closed tracheal cannula for 90 seconds.
8 ,, ,, 89 ,,

With doses of the $\frac{1}{100}$ cub. centim. (= 0·0086 grm.; NO_2 = 0·00378 grm.) the fall of pressure averaged 49 millims., placing the drug high in the list of the bodies examined. Slightly stronger than iso-butyl nitrite, it was much beyond primary butyl nitrite and α-amyl nitrite in its activity. The reduction of pressure is succeeded by a slower rise, so that after a lapse of 5 minutes from the commencement of inhalation there is frequently a deficiency of 11 or 12 millims. when contrasted with the original pressure. The acceleration of the pulse is greater than after iso-butyl nitrite.

Intra-vascular Injection.—The *intra-vascular injection* of tertiary butyl nitrite in doses of $\frac{1}{100}$ cub. centim. was found on examination to fall far short of inhalation in the extent to which it produces a fall of pressure, so much so that it is much feebler than secondary butyl nitrite, and slightly feebler than the iso-butyl compound. It is also weaker than tertiary amyl nitrite, but retains its superiority over normal butyl nitrite.

But though the fall of pressure is from 35 to 40 per cent. less than after inhalation of a like dose, the reduction of pressure is frequently maintained for a considerable time.

The pulse is accelerated to a less extent than after inhalation averaging six beats per minute, but the acceleration commences from 5 to 8 seconds later after injection than after inhalation.

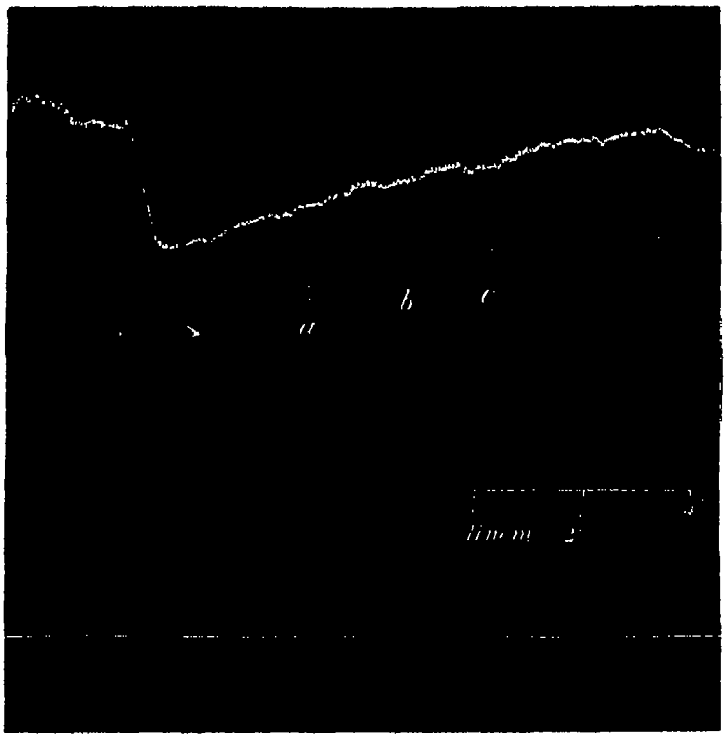
In this respect it stands close to iso-butyl nitrite. The following may be taken as the usual variations of pulse and blood-pressure due to the injection of the $\frac{1}{100}$ cub. centim. of this drug.

Cat. of 5 lbs. Etherized. Administered $\frac{1}{100}$ cub. centim. in 5 cub. centim. salt solution. Pressure fell 24 millims. in 5 minutes is −9, in 7·45 minutes is normal. Tracing 12.

	Time.	Pulse.
	secs.	
Before drug	0	148
During injection of $\frac{1}{100}$ cub. centim. tertiary butyl nitrite into femoral vein	5	149
	15	147
	20	148
	25	149
	30	151
	40	154
	50	154
	70	147
	90	147
	110	145
	180	148

As has been already stated the respiration is retarded, or even temporarily suspended, by inhalation of this nitrite (see tracing 10*b*).

Tracing 12.



Injection by femoral vein of $\frac{1}{100}$ cub. centim. iso-butyl nitrite in 5 cub. centim. salt solution.

The Propyl Nitrites.

Primary propyl and secondary propyl nitrites were examined.

Primary Propyl Nitrite.

The most obvious fact concerning primary propyl nitrite is the small degree of activity it possesses in reducing blood-pressure, when contrasted with many of the nitrites already examined. It is very inferior in its effect to the secondary compound, which is amongst the most active of the nitrites. The fall it occasions is not rapid, the lowest point being reached in from 33 to 38 seconds after inhalation commenced. Recovery to the original level takes place somewhat sooner than the recovery succeeding secondary propyl nitrite, although the latter occasions a much greater fall.

The recovery after pure amyl nitrite in contrast experiments was shown to be slower. Slight retardation of the pulse during early primary nitrite of propyl inhalation is a frequent preliminary to the succeeding acceleration. This acceleration, after doses of $\frac{1}{30}$ to $\frac{1}{40}$ cub. centim., amounts to from 8 to 12 beats per minute. The chief acceleration occurs immediately after the greatest reduction of pressure, *i.e.*, about 40 seconds after the inhalation is begun.

In from 2½ to 3 minutes the pulse usually reaches its original rate or falls below it.

Experiment.—Small cat of 4 lbs. Ether steadily given from ether bottle. Artificial respiration.

Before inhalation, pressure 104; fell on administration of $\frac{1}{38}$ cub. centim. (= 0·0234 grm.; NO_2 = 0·0121 grm.) to 72, and regained the original level in course of 5 minutes. The lowest pressure was in 32 seconds after inhalation was begun.

	Time.	Pulse.
	secs.	
Before inhalation	. .	171
After inhalation	10	169
	20	170
	30	177
	40	179
	50	180
	60	180
	70	176
	80	174
	95	174
	145	174
	165	170
	175	168
	185	166

Doses of $\frac{1}{100}$ cub. centim. do not fail to cause a fall of pressure, and here it may be remarked how surprising it is that so small a variation exists in the reaction shown by animals to such widely different doses as the $\frac{1}{30}$ and $\frac{1}{100}$ cub. centim.; the smaller often coming near in its action to the larger dose.

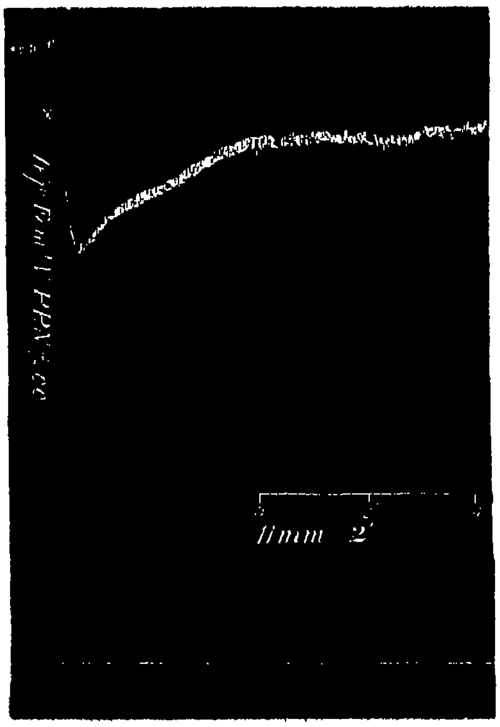
Inhalation of $\frac{1}{100}$ cub. centim. (= 0·0089 grm.; NO_2 = 0·0046 grm.) causes an average fall of 18·5 millims. accompanied by a pulse acceleration of about 3 to 6 beats per minute, while the pressure recovered within the exceptionally short time of three minutes from commencing inhalation. These figures enable us to classify primary propyl nitrite as one of the least active in reducing pressure and in maintaining the reduction, while they indicate only a feeble tendency to produce acceleration.

Intra-vascular Injection.—The relatively feeble effect which this drug produces on inhalation does not fully extend to administration by intra-vascular injection.*

Intra-venous Injection causes a slight rise of pressure, succeeded by a rapid, extensive fall, and a gradual recovery.

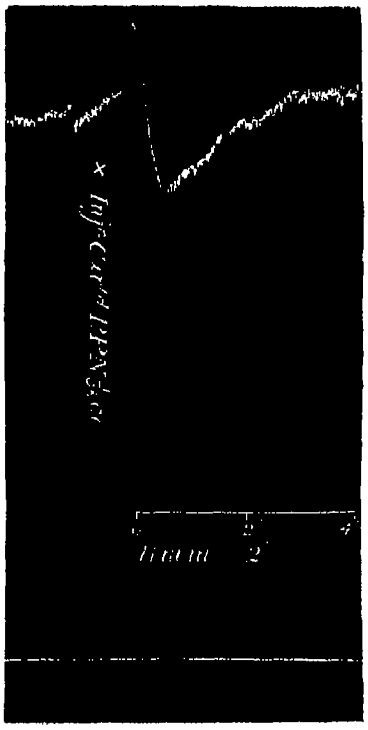
The following experiment will serve to illustrate the points under consideration, tracing 13*a*.

Tracing 13*a*.



Injection by saphenous vein of $\frac{1}{38}$ cub. centim. primary propyl nitrite in 5 cub. centims. salt solution.

Tracing 13*b*.



Injection by cranial end of carotid artery of $\frac{1}{38}$ cub. centim. primary propyl nitrite in 2 cub. centims. salt solution.

Injection of primary propyl nitrite $\frac{1}{38}$ cub. centim. in 5 cub. centims. salt solution by saphenous vein.

Original pressure 118·5 millims.

After injection rises in 8 seconds to 122.

Falls in 45 seconds to 81.

In	2	minutes	has	risen to	92
„	4	„	„	„	100
„	8	„	„	„	102
„	10	„	„	„	105

---

* Reference must be made to the section dealing with pure amyl nitrite for the mode of administration.

	Time.	Pulse.
	secs.	
Before injection . . .	..	156
During " . . .	20	155
After " . . .	5	155
	20	155
	40	154
	60	152
	120	152
	200	152
	240	150
	280	153

Intra-venous Injection of $\frac{1}{100}$ cub. centim. The administration of this small dose causes a fall of pressure slightly superior to that due to inhalation, but the difference is not marked.

The fall averages 20 millims., and the return to the normal pressure is later in occurring, so that in 5 minutes it is usually 4·5 millims. below the normal. This slow rise is accompanied by only a very slight pulse acceleration, if any, the average not exceeding two per minute.

3.3.90.—Cat of 5 lbs. Cannula in femoral vein, &c. Steady inhalation of ether. $\frac{1}{100}$ cub. centim. primary propyl nitrite in 5 cub. centims. salt solution injected into femoral vein. Pressure fell 19 millims.; in 6 minutes it is − 4.

	Time.	Pulse.
	secs.	
Normal	..	126
Injection	5 10 15	126 124 125
	20	126
	30	125
	40	126
	60	126
	180	126

Intra-arterial Injection. (Cranial end of carotid.)—This method of administration caused a powerful rise, succeeded by a gradual fall. The pressure recovered comparatively soon. Tracing 13*b*.

Experiment.—Injection into cranial end of carotid artery of $\frac{1}{38}$ cub. centim. primary propyl nitrite in 2 cub. centims. salt solution.

Original pressure was 110 millims.

On injection pressure rose in 33 seconds to 124
„ „ fell „ 70 „ „ 91
„ „ rose „ 120 „ „ 101·5
„ „ „ „ 240 „ „ 108

	Time.	Pulse.
	secs.	
Before injection	0	156
During injection of $\frac{1}{32}$ cub. centim. of primary propyl nitrite	20	157
After injection	30	157
	40	155
	65	156
	100	154
	115	152
	140	153
	200	154

In each of these experiments the pulse had little or no tendency to accelerate. The intra-arterial injection was immediately followed by a strong rigor, which had not been produced by other nitrites injected in this manner. The relationship of the action of the drug administered by injection into the vessels and by inhalation is not parallel here with the relationship existing in the case of pure amyl nitrite and of iso-butyl nitrite respectively.

Effect on Respiration.—Although the inhalation of primary propyl nitrite may cause some retardation of respiration, the marked effect occasioned by the butyl compounds has not been observed.

Secondary or Iso-Propyl Nitrite.

This substance when administered by inhalation is one of the most active members of the series in its power of reducing pressure. The fall recorded by the manometer is both rapid and extensive, so that after an inhalation of $\frac{1}{100}$ cub. centim. a reduction of pressure somewhat exceeding that of the iso-butyl nitrite (the latter being usually almost identical with that of secondary butyl nitrite) is observed; for this dose the fall averages about 50 millims.

The speed of reduction is considerable, the lowest pressure being reached in 30 to 35 seconds after the commencement of inhalation. The greater part of the reduction is, however, accomplished during the first 20 seconds, while in the last 10 seconds the decline is scarcely perceptible. The percentage speed of the fall in two observations taken from one experiment averages as follows :—

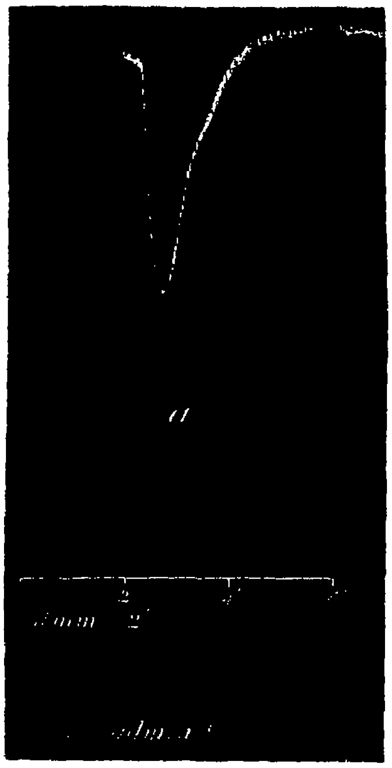
Usual preparation for experiment. $\frac{1}{80}$ cub. centim. (= 0·029 grm.; NO_2 = ·0045 grm.) secondary propyl nitrite administered by inhalation. The fall began in 4·5 seconds.

In the ensuing 10 seconds fall = 57·5 per cent. of the total reduction.
" 10 " (20) " = 30 " "
" 10 " (30) " = 12 " "

The fall was therefore practically at an end by the 35th second. In this rapidity of action iso-propyl is not far removed from iso-butyl nitrite, though, as already stated, a close comparison of the effects of the two bodies shows the latter to be somewhat less powerful as a reducer of pressure.

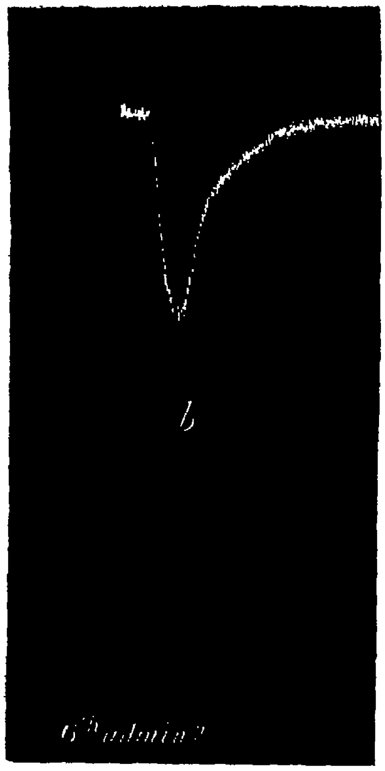
Another point of resemblance lies in the fact that the recovery of pressure is rapidly brought about by the return of tone in the arterioles, with or without a marked acceleration in pulse rate. The rise of pressure towards the normal is at first rapidly accomplished, but after repeated administrations without the production of a serious permanent fall of pressure, the recovery of the normal pressure becomes much more gradual after the administration of the nitrite.

Tracing 14*a*.



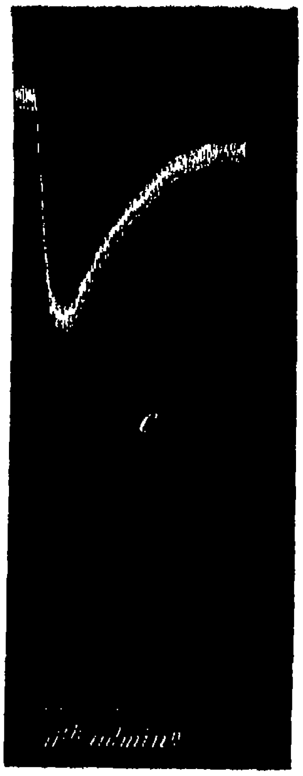
Secondary propyl nitrite $\frac{1}{100}$ cub. centim. First inhalation.

Tracing 14*b*.



40 minutes later, the sixth administration.

Tracing 14*c*.



52 minutes later than 14*b*, the eleventh administration.

The following Table gives the results of three administrations of secondary nitrite of propyl in an experiment in which no other nitrite was given.

Time.	Dose.	Fall of pressure.	Period of recovery of pressure.
	cub. centim.	millims.	secs.
(1st administration) *a* 5 minutes	$\frac{1}{100}$	47	109
(6th administration) *f* 40 minutes	"	40	153
(11th administration) K 92 minutes	"	42	228 reached − 8 and did not rise higher

It will be observed that, after repeated administration, the later part of the recovery of pressure is affected rather than the earlier part, but this may also become retarded. During the inhalation of the drug retardation is a frequent first effect, especially if the original rate is rapid. Subsequent acceleration is by no means extensive; it averages 4 beats per minute after administration of $\frac{1}{100}$ cub. centim. Increase of dose causes a further acceleration (7 beats per minute after $\frac{1}{30}$ cub. centim.), and somewhat increases the fall and retards the rise of pressure.

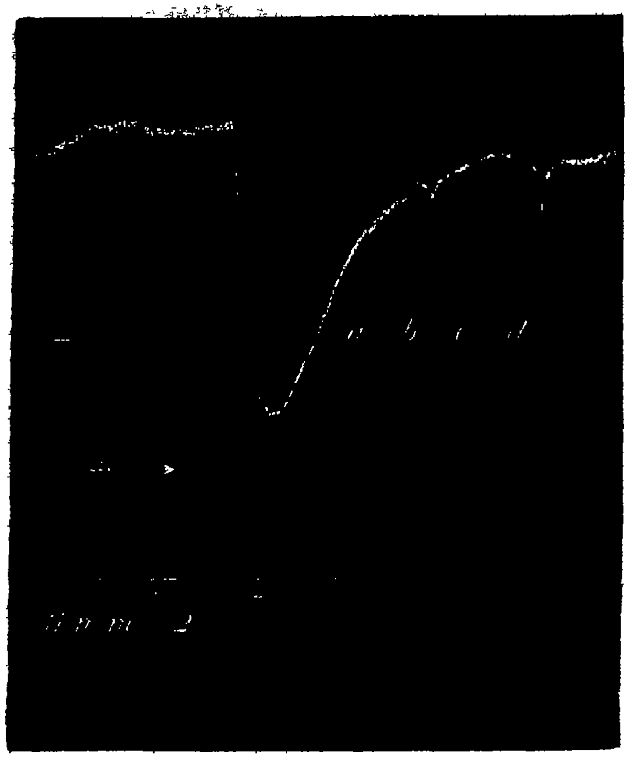
The powerful pressure-reducing effect of secondary propyl nitrite when administered by inhalation is not equalled by that observed after injection into the vessels, although its relative effect is sufficient to place it near the head of the list. After an injection of $\frac{1}{30}$ cub. centim. (= 0·029 grm.; NO_2 = 0·0150 grm.), the average fall is 43 millims.; while after a dose of $\frac{1}{100}$ cub. centim. (0·087 grm.; NO_2 = 0·0045 grm.) it is from 30 to 33, the first indication of reduction being observed in 11 seconds, the minimal pressure occurring in 50 seconds, the injection being completed in 18 to 20 seconds.

The following experiment contrasts the effect of inhalation and injection:—

24.2.90. Cat of 5 lbs. Usual preparation. Receiving ether steadily.
Pressure fell 60 millims.; in 5 minutes was — 3. Tracing 15*a*.

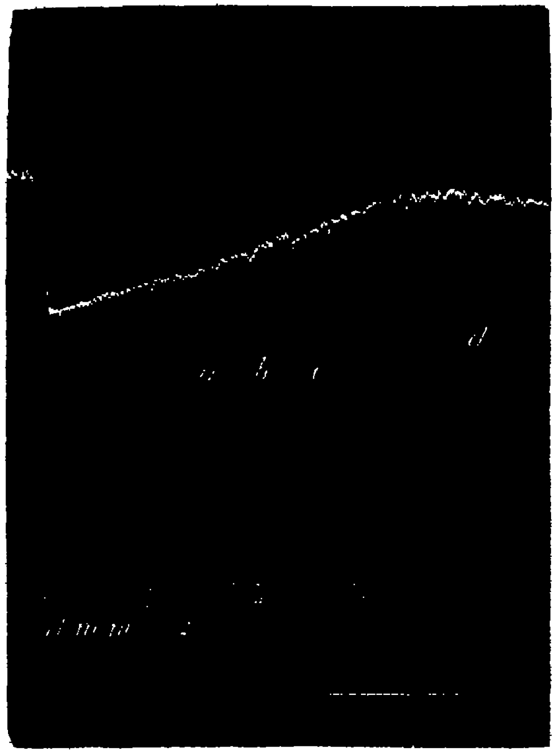
	Time.	Pulse.	Respiration.
	secs.		
Before inhalation	0	134	32
Began inhalation of $\frac{1}{30}$ cub. centim. (= 0·0108 grm.; NO_2 = 0·057 grm.) secondary propyl nitrite	5	132	
	15	133	
	25	132	32
	90	127	31
	420	125	33
	520	136	34

Tracing 15*a*.



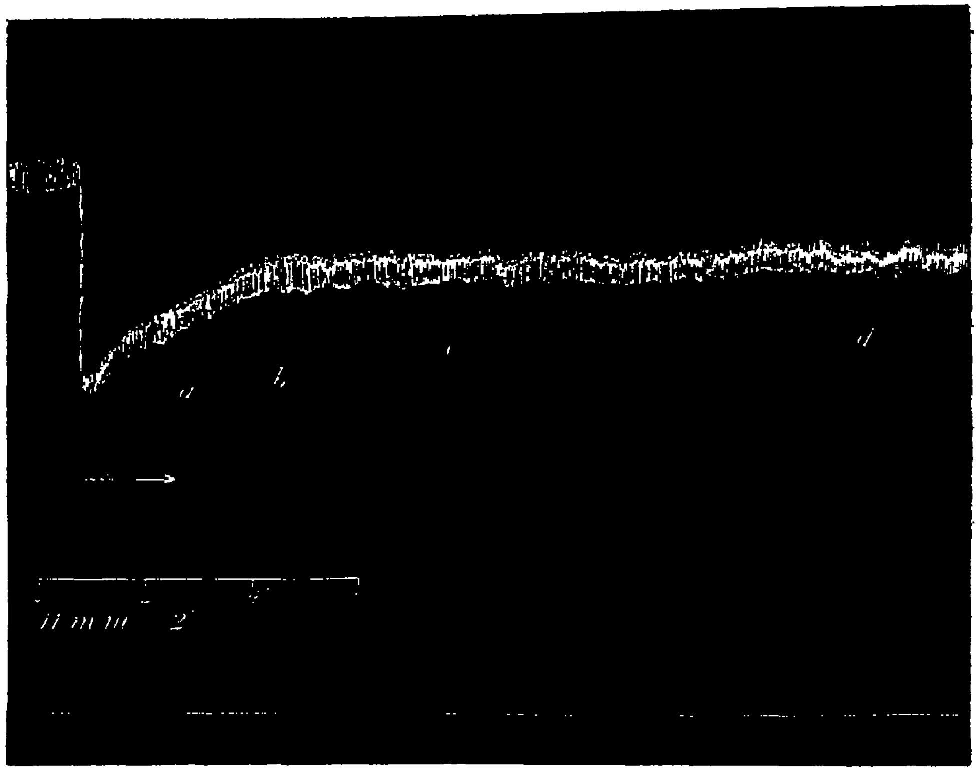
Inhalation of $\frac{1}{80}$ cub. centim. secondary propyl nitrite.

Tracing 15*b*.



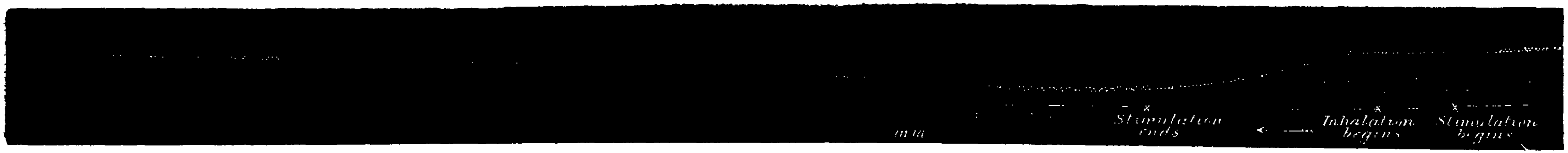
Injection into femoral vein of $\frac{1}{100}$ cub. centim. secondary propyl nitrite.

Tracing 16.



Injection by femoral vein of $\frac{1}{80}$ cub. centim. secondary propyl nitrite.

Tracing 17



Inhalation of $\frac{1}{80}$ cub. centim. secondary propyl nitrite. Reduced one-half, preceded and accompanied by stimulation of the central end of the sciatic nerve. The upper line shows pulse and pressure, the middle respiration, the lowest shows signal record of time of stimulation. See also pressure record taken on slow drum.

24.2.90. *Intra-venous Injection.*—Pressure fell 30 millims.; in 7 minutes 16 seconds was − 4 millims. Tracing 15*b*.

	Time.	Pulse.	Respiration.
	secs.		
Before administration	0	124	32
Injected $\frac{1}{100}$ cub. centim. secondary propyl nitrite into femoral vein .	5	123	
	15	118	
	20	117	
	45	123	
	70	123	34
	85	120	
	95	120	31
	180	105	35
	240	104	
	300	101	31

A larger dose of secondary propyl nitrite given by injection causes a moderate primary fall. The recovery after this may be tolerably rapid at first, but subsequently the pressure rises very slowly, so that it is often a considerable time before the original level is reached.

13.2.90. Cat of medium size. Steadily etherized. Usual preparation. Inhalation of $\frac{1}{80}$ cub. centim. secondary propyl nitrite, having occasioned a fall of 54 millims. Almost complete recovery in 5 minutes.

An injection of $\frac{1}{30}$ cub. centim. secondary propyl nitrite in 5 cub. centims. salt solution was made into the femoral vein. Tracing 16.

The pressure fell 45 millims.

In 4 minutes was 21 millims. below the original level.
„ 5 „ „ 21 „ „ „ „
„ 8 „ „ 19 „ „ „ „
„ 10 „ „ 19 „ „ „ „

The pressure remained permanently reduced.

	Time.	Pulse.
	secs.	
Before	0	123
During injection of $\frac{1}{80}$ cub. centim. secondary propyl nitrite	5	122
	10	120
	20	119
	10	117
	15	
	20	122
	30	123
	40	
	50	
	75	122
	420	114
	900	116

Respiration.—The effect of a single administration of secondary propyl nitrite is first to retard, then to accelerate the respiration; this phase is succeeded by a period during which acceleration without any retardation results, and this, again, is succeeded by a tendency to considerable retardation, when the administration has been frequently repeated. The effect produced on respiration by this body is much less marked than that of the butyl compounds.

If in the early stage of retardation produced during the first administration the central end of the sciatic nerve is strongly stimulated, acceleration and deepening of the respiration results; but the fall of the pressure is not prevented, not even diminished. Here it is interesting to observe that the respiratory centre does not cease to respond to the stimulation until a distinct fall of pressure has taken place.

(19.6.90.) Cat of 5 lbs. Steadily etherized. Breathing rapid throughout. Tracing 17.

On inhalation pressure fell 122-84 (38 millims.), in 196 seconds is normal and passes slightly beyond it, so that in 5 minutes it is 124 millims.

	Time.	Pulse.	Respiration.
	secs.		
Before inhalation . . .	..	186	52
Sciatic stimulation . . .	0	187	75
Sciatic stimulation and inhalation of secondary propyl nitrite, $\frac{1}{80}$ cub. centim.	5	186	84
	10	180	
Stimulation ended . . .	20	178	75
	30	177	
	40	183	42
	50	183	46
	60	189	45
	80	187	45

Ethyl Nitrite.

Since the manipulation of this substance is attended with no small difficulty because of its low boiling point (17° C.), the bottle, pipette, and tube into which the nitrite was carried were thoroughly cooled with ice.

The drug was usually introduced into a cooled bulb with tubing at both ends closed by screw clamps. The tubing was brought into connection with the inhalation apparatus, a water valve being placed distally in relation to it, and the tracheal cannula valve permitting only of expiration was employed as usual.

Its action was tested in experiments in which it was used alone as well as in other experiments in which other nitrites were also used, whose position had been approximately ascertained.

Ethyl Nitrite by Inhalation.—This nitrite when administered by inhalation is not found, as regards its power of reducing pressure, to be a prominent member of the nitrite series.

With doses of $\frac{1}{100}$ cub. centim. (= 0·0089 grm.; NO_2 = 0·00545 grm.) the average fall in pressure is between 19 and 20 millims., and the chief reduction is brought about in 25 to 28 seconds after the commencement of inhalation.

The most usual mode of return towards the normal is by a gradual elevation of pressure which approaches the normal in 6 to 8 minutes, but in exceptional cases a more rapid reaction ensues and an equal amount of recovery may occur in 3 minutes. In the latter case the variation is not due to a greater acceleration of pulse or any change in respiration.

As a rule acceleration of the pulse occurs up to 7 per minute, and it is not long maintained. The respiration is retarded. Larger doses, viz., the $\frac{1}{40}$ cub. centim. to $\frac{1}{30}$ cub. centim. given by inhalation increase to some extent the fall of pressure, and tend, as in smaller doses, to produce a prolonged reduction of pressure. In exceptional cases the return is more active, thereby resembling the effect of a smaller dose of iso-butyl nitrite.

One such result may be quoted.

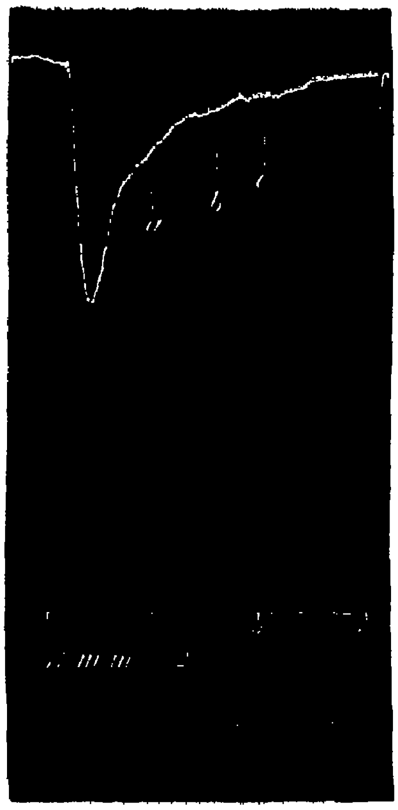
(17.3.90.)—Cat of 4½ lbs. Steadily etherized. Tracing 18.

On inhalation of $\frac{1}{34}$ cub. centim. (= 0·0261 grm.; NO_2 = 0·0160 grm.) of the ethyl nitrite, the pressure fell 44 millims. (127 to 83); in 120 seconds it rose again to 119 millims., and in 196 seconds to 122 millims. or within 5 millims of the normal. The initial fall was observed 5 seconds after the commencement of inhalation, and the lowest point was reached in 25 to 30 seconds, a rise immediately occurring.

The course of the pulse and respiration may be traced from the following figures.

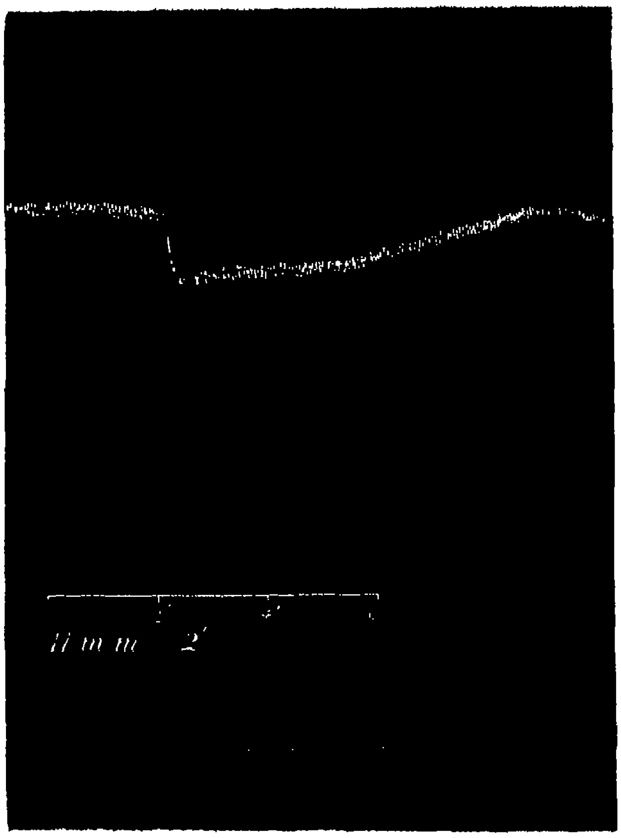
	Time.	Pulse.	Respiration.
	secs.		
Before inhalation . . .	..	135	33
Inhalation of $\frac{1}{34}$ cub. centim. commenced	0		
	5	136	31·5
	10	138	
	15	138	
	20	138	27
	30	137	
	40	135	
	50	133	27
	60	132	
	90	111	22
	160	117	22
	220	122	25

Tracing 18.



Inhalation of $\frac{1}{34}$ cub. centim. ethyl nitrite.

Tracing 19.



Inhalation of $\frac{1}{50}$ cub. centim. ethyl nitrite.

During inhalation of the smaller dose a slight retardation of the pulse is frequently noticed, and occasionally the pulse remains subnormal throughout; but usually this phase of slowing is only of short duration, and is succeeded by a slight acceleration, which reaches its maximum about 35 seconds after the commencement of inhalation.

This increase may be to the extent of 6 to 10 beats, and the respiration appears to be slowed at first, and, like the pressure, recovers itself gradually.

We will now give an illustration of the prolonged reduction of pressure which has been frequently observed. In this case the primary reduction of pressure was decidedly below the average.

(31.5.90.) Cat of 7 lbs. Receiving ether regularly. Vagi intact. Breathing natural. Tracing 19.

Blood-pressure 104. Pulse 154. Respiration 25·5.

Administered $\frac{1}{50}$ cub. centim. (= 0·0178 grm.; NO_2 = 0·0109 grm.) ethyl nitrite.

Pressure began to fall in 4 seconds; fell to 90 millims. in 30 to 35 seconds.

In 2 minutes it rose to 92 millims.
„ 4 „ „ 96 „
„ 6 „ „ 100·5 „ .

	Time.	Pulse.	Respiration.
	secs.		
Before inhalation . . .	..	156	23·5
Inhalation	0		
	5	156	22·5
	10	156	
	20	153	24·5
	25	154	
	30	160	17
	35	158	
	40	156	
	45	156	
	50	156	19·5
	55	156	20
	100	156	21·5
	110	..	22·5
	140	158	24
	360	159	24

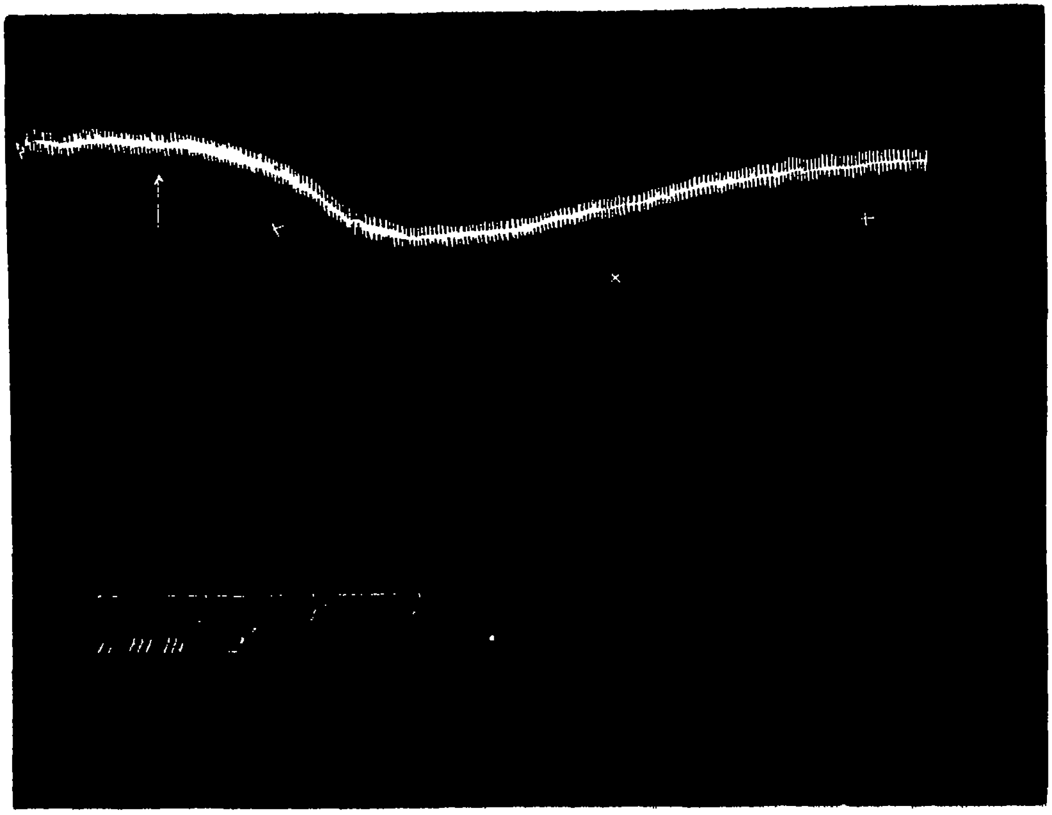
It will be observed in this experiment that a marked retardation of respiration followed inhalation, but there was a return to the normal in 2 minutes.

Ethyl nitrite administered by (*a*) hypodermic and (*b*) by intra-vascular injection.

(17.7.90.) (*a*) *Hypodermic Injection.*—The absorption of the nitrite when injected beneath the skin of the flank proceeds with considerable rapidity. In the experiment quoted, a distinct fall of pressure was observed 49 seconds after the injection of $\frac{1}{50}$ cub. centim. commenced. The time occupied by the injection was 20 seconds. The lowest point was reached 3 minutes later. Tracing 20.

Original pressure 118 millims.
3 minutes fell to 107 „
4·5 „ „ „ 100 „
8 „ rose to 106 „
12 „ „ „ 112 „
14 „ „ „ 113·5 „

Tracing 20.



Hypodermic injection of $\frac{1}{50}$ cub. centim. ethyl nitrite.

	Time.	Pulse.
	secs.	
Original pulse rate	..	140
During injection	20	140
After injection completed . . .	10	136
	20	136
	30	136
	40	139
	50	139
	60	139
	70	138
	110	139
	130	134
	140	133
	150	132
	400	132
	580	137
	740	141

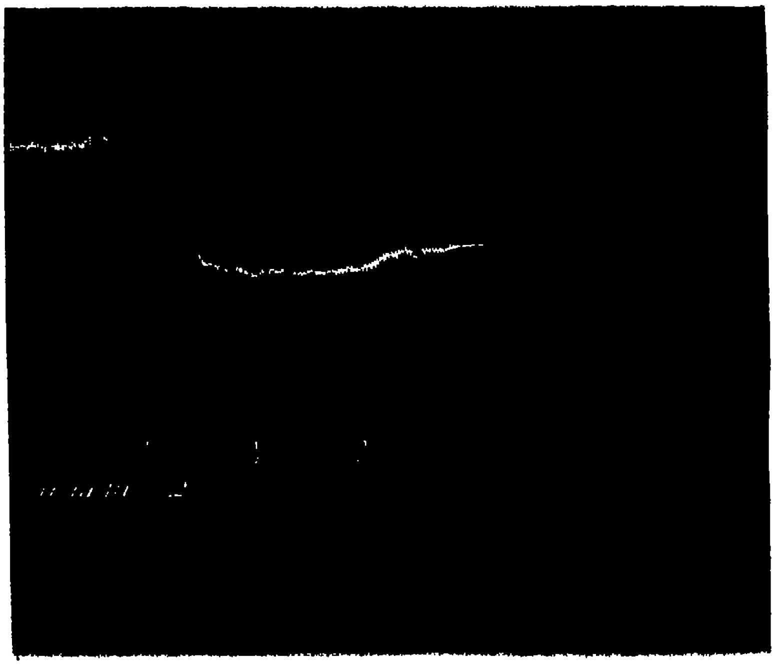
Intra-vascular Injection.—The fall after this method of administration is prompt and extensive, and a prolonged subnormal level of the pressure ensues during which the rise is very gradual.

By intra-venous injection a powerful effect may be produced on respiration, causing its temporary arrest, or, if the dose be larger, its permanent suspension. (After one administration a singular effect was observed. The blood-pressure had fallen 28 millims. after injection of $\frac{1}{38}$ cub. centim. ethyl nitrite, and remained at this level; respiration became rapidly feeble and ceased; the pressure fell still further in spite of artificial respiration, no tendency to spontaneous respiration appearing

5 minutes after the injection. When the vagi were divided the pressure rose and respiration was immediately resumed.)

An experiment will now be quoted which illustrates the usual effect of injection.

Tracing 21.



Intra-venous injection of $\frac{1}{38}$ cub. centim. ethyl nitrite.

(4.6.90.)—Cat of $5\frac{1}{4}$ lbs. Steadily etherized. Cannulæ in carotid artery and saphenous vein. Original pressure 86, after injection of $\frac{1}{38}$ cub. centim. (= 0·0234 grm.; NO_2 = 0·0143 grm.) ethyl nitrite by saphenous vein, fell to 60 millims. Tracing 21.

In 2 minutes pressure was 59 millims.
„ 4 „ „ „ 62·5 „
„ 6 „ „ „ 65 „

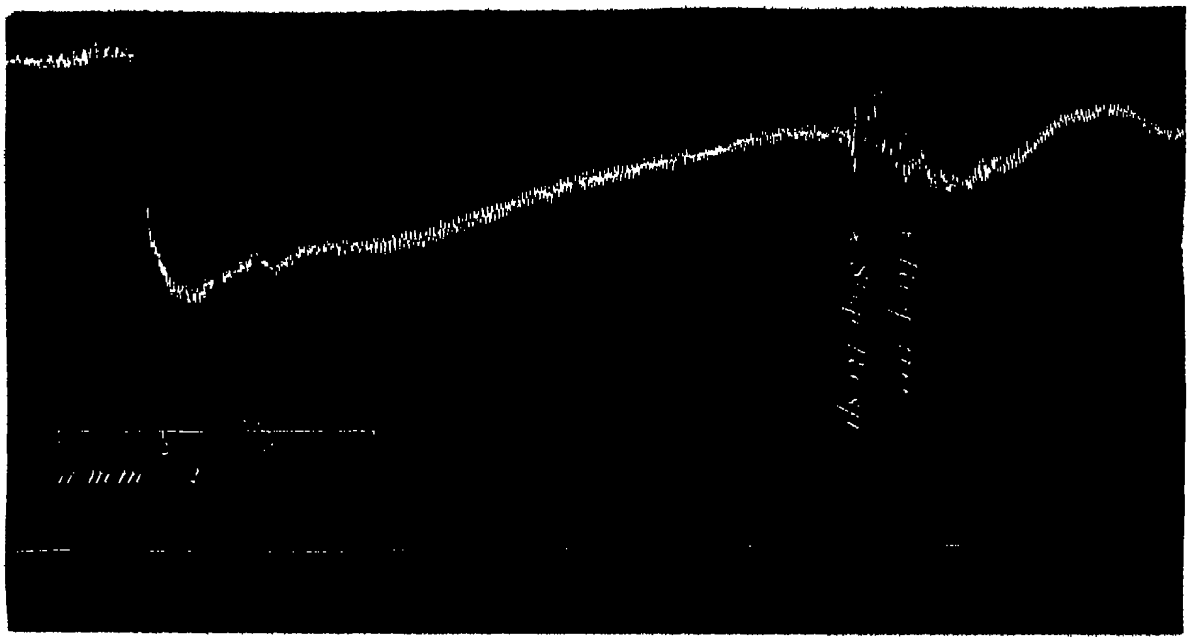
	Time.	Pulse.
	secs.	
Before injection	. .	161
During „	25	159 to 156
After „	15	154
	30	155
	50	154
	80	154
	110	154
	140	150
	230	155
	300	155

In this experiment the initial reduction in pressure was preserved for a considerable time.

It is also seen that a decided fall in the pulse rate was associated with the action of this drug after intra-venous injection, although in two minutes afterwards there was a feeble return towards the normal.

Another case in which a larger dose was given may be contrasted with the experiments in which the administration was by inhalation.

Tracing 22.



Injection of $\frac{1}{18}$ cub. centim. ethyl nitrite in 5 cub. centims. salt solution into femoral vein. Showing effect of suspending respiration.

(31.5.90.) Injection of $\frac{1}{38}$ cub. centim. (= 0·0488 grm.; NO_2 = 0·0302 grm.) ethyl nitrite in 5 cub. centims. salt solution into femoral vein. Tracing 22.

Pressure originally 100 fell to 51 (= 49) millims.

In	2	minutes	the pressure	was	58
„	4	„	„	„	60·5
„	6	„	„	„	64
„	8	„	„	„	71
„	10	„	„	„	77
„	12	„	„	„	81
„	16	„	„	„	84

Arrest of respiration caused large waves in the pressure, but no permanent rise of pressure.

	Time.	Pulse.	Respiration.
	secs.		
Before injection	..	144	27
During injection of $\frac{1}{18}$ cub. centim. (= 0·0556 grm.; NO_2 = 0·034 grm.) ethyl nitrite into saphenous vein	0 10	144	27
Injection ended	20	142	22
	30	138	15
	40	136	15
	50	140	15
	65	144	Respiration becoming very rapid.
	70		
	80	138	
	95	144	16·5 Very faint.
	105	..	No respiration.
	125	..	4
	140	..	4·5
	180	..	9

The fall of pressure commenced 12 seconds after injection, and attained its lowest point in 55 seconds. The lasting retardation of respiration played an important part in the prolonged reduction of pressure.

One cannot but assign to the nitrite of ethyl a peculiar place among the other substances of the series examined. When given by inhalation the fall of blood-pressure, although inconsiderable, is frequently of prolonged duration. When injected subcutaneously the fall is distinct and enduring, whilst after intra-venous injection there is a prompt fall associated with even slower recovery of pressure and usually with retardation of pulse.

Methyl Nitrite.

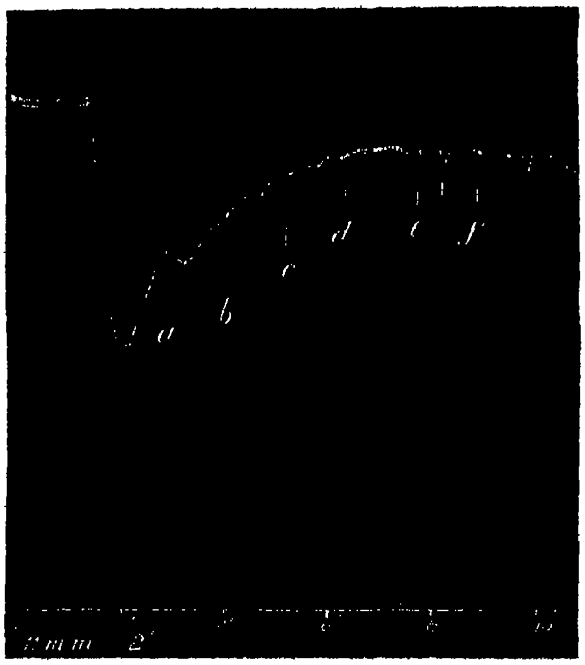
Methyl nitrite was employed in this series of experiments in the gaseous form. It was introduced, as has been already explained, at the temperature and pressure noted into spindle-shaped glass bulbs, the ends of which were drawn out into fine points. Such bulbs were prepared for experimental use by drawing over their ends rubber tubes provided with clamps, securing them by ligatures, and connecting them with the lateral inhalation tube and the water-valve bottle. The thin glass ends were fractured inside the rubber tubes when all was ready for inhalation; the clamps opened, and, last of all, the stopcock proximal to the animal turned on at the same instant as the ether bottle or air tube, as the case might be, was turned off. The bulb and system of tubes were rapidly emptied of the nitrite, and the fall of blood-pressure promptly ensued. By this method, measured quantities of nitrite were administered with perfect precision.

In all cases the primary fall of pressure was well marked, though not of great extent when contrasted with the effect of a comparative dose of many other nitrites.

Usually, there was a considerable pause before the normal pressure was recovered, the return being only gradually accomplished. (The return in the experiment first quoted was unusually rapid.) Acceleration of the pulse was not a prominent feature in the action of methyl nitrite; three to four beats per minute was frequently the full amount of acceleration induced by about $\frac{1}{50}$ cub. centim. of the liquid nitrite. A great retardation of the pulse was observed in a large precentage of cases of inhalation, whilst the breathing was affected in a similar manner. Several inhalations terminated fatally.

Some experiments showing the results of inhalation will now be described.

Tracing 23*a*.



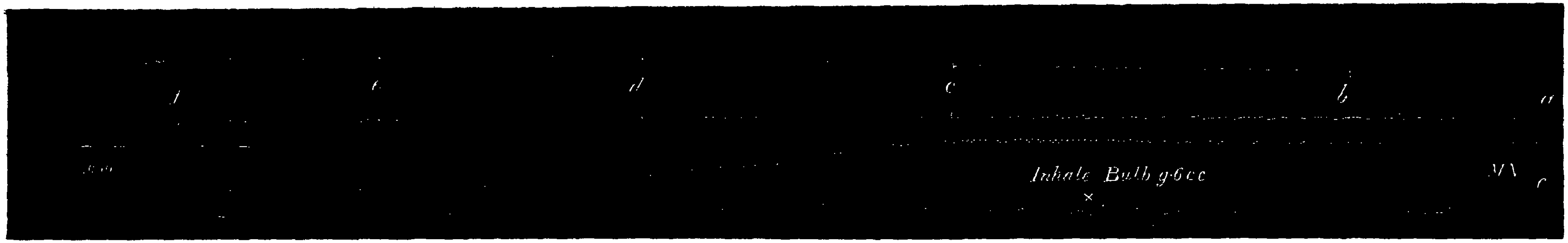
Inhalation of 0·0245 grm. methyl nitrite, the letters correspond to those in the quick tracing 23*b*.

Experiment.—Large cat. Steadily etherized. Tracings 23*a* and 23*b*. Administered 9·6 cub. centims. bulb of methyl nitrite from tracheal cannula (= $\frac{1}{85}$ cub. centim. liquid) (= 0·0245 grm.; NO_2 = ·0185 grm.).

Original pressure, 98 millims., fell to 48 = fall of 50 millims.

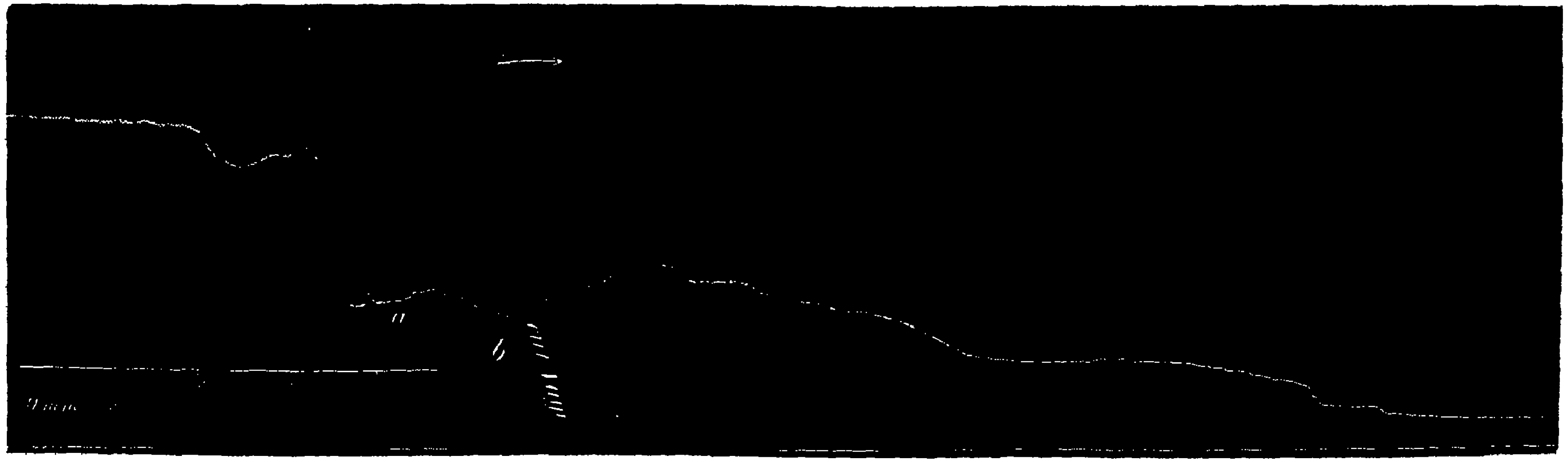
In 2 minutes rose to 67 millims.
,, 4 ,, ,, 86 ,,
,, 6 ,, ,, 89 ,,
,, 8 ,, it was 88 ,,

Tracing 23*b*.



Inhalation of methyl nitrite (9·6 cub. centims. bulb). Reduced one-half. The upper tracing is continuous with the lower. The upper line in each pair shows pressure and pulse; the lower respiration. The letters correspond with those on the slow tracing 23*a*.

Tracing 24.



Inhalation of methyl nitrite (10 cub. centims. bulb) at star. The vagi are cut where indicated. This record is taken on the slow cylinder by a mercuria manometer, and is to be read from left to right.

	Time.	Pulse.	Respiration.	
	seconds.			
Before inhalation . . .	..	130	33	
Methyl nitrite 9·6 cub. centims. bulb, inhalation begun, molecular equivalent to $\frac{1}{35}$ cub. centim. (liquid)	0			
	5	131		
	10	132	33	
	20	132		
	25	135	21	
	35	135	27	
	40	135	..	Breathing irregular
	45	133	..	Breathing stopped
	55	128		
	65	124		
	75	..	..	Breathing recovered
	87	122	23	
	160	128	20	
	230	127		
	300	128	27	
	360	112	26	
	450	112	28	

The slowing of respiration leading to entire suspension is here a noticeable effect. The pause was only temporary, and terminated after 30 seconds, the respiration resuming a fairly rapid rhythm.

The result of inhalation next recorded shows the alternative form of recovery. It indicates a slighter primary effect than the last, succeeded by a slow but gradual return of pressure.

Experiment.—(2.) Medium sized cat. Steadily etherized. Administration of 10·2 cub. centims. bulb, equivalent to $\frac{1}{37}$ cub. centim. of liquid (= ·0261 grm.; NO_2 = ·0196 grm.). Bulb connected with inspiratory apparatus; administration as in preceding experiment.

Original pressure 142 fell to 106 millims., fall of 36 millims.

In 4 minutes pressure was 108 millims.
" 6 " " " 116 "
" 8 " " " 124 "
" 10½ " " " 136 "
" 13 " " " 139 "
" 15 " " " 141·5 "

	Time.	Pulse.
	secs.	
Before inhalation	..	153
Inhalation begun	0	
	5	156
	10	
	15	158
	20	159
	25	156
	30	153
	35	
	55	150
	75	
	95	147
	130	143
	240	143
	360	140
	480	147

The following is an example of the experiments already referred to in which inhalations terminated fatally.

(14.3.90.) Half-grown cat. Usual preparation. Steadily etherized. Administration of 10 cub. centims. bulb (= ·0256 grm.; NO_2 = ·0192 grm.). Bulb in connection with respiratory apparatus, water-valves, &c. Tracing 24.

On inhalation the pressure fell from 67 to 32 millims., in 120 seconds it rose to 35 and in 15 seconds more to 36; it then declined until the vagi were divided (at 284 seconds) when it rose to 41, but thereafter declined steadily, death resulting in spite of artificial respiration.

	Time.	Pulse.	Respiration.
	secs.		
Before inhalation	..	138	14
Inhalation begun	0		
	5	138	
	10	136	14·5
	25	136	
	30	137	
	40	139	
	50	138	
	65	139	16
	85	140	
	145	..	14
	220	80	2
Vagi divided	287		
	330	74	
	390	..	Artif. resp.

Although artificial respiration was had recourse to the action of the heart gradually became feebler, and the pressure having fallen to 22 millims. 14 minutes 30 seconds after inhalation commenced, artificial respiration was suspended, and death ensued. There need be no doubt that such a dose is a dangerous one, even for a fully grown animal.

In one instance inhalation of a 5 cub. centims. bulb (= ·0178 grm.; NO_2 = ·0096 grm.) nearly proved fatal.

In this experiment made upon a cat of 6¾ lbs. the pressure fell at once 50 millims. (98 to 48 millims.), the frequency of the pulse was reduced one-half in 55 seconds, viz., from 139 to 67, two or three beats occurring in groups succeeded by a long diastolic pause. The respiration, after four or five deep breaths had been taken, was reduced to an occasional gasp. Artificial respiration was used and the vagi divided; but gasping occurred after, just as before vagotomy. The pulse which had increased to 96 under artificial respiration rose 4 beats more when the vagi were divided. The pressure never rose higher than 66 millims., and thereafter gradually declined 35 minutes after inhalation, to 34 millims., when another small dose of methyl nitrite caused cardiac arrest.

Intra-vascular Injection of Gaseous Methyl Nitrite.—By connecting a bulb containing a given volume of methyl nitrite with the rubber tubing tied on the femoral vein cannula, which had been previously filled with salt solution, and forcing out the gas before salt solution discharged from a syringe into the other end of the bulb, it became a simple matter to introduce the nitrite into the femoral vein, and so to study its action.

All such injections terminated fatally, even though they were made very gradually. Although no gas bubbles could be detected in the right side of the heart, the fatal result was very probably, in some measure, due to embolism. Larger quantities of atmospheric air were, however, injected at the same slow rate into the central end of the vein without death resulting.

A marked retardation of the pulse preceded the fatal action of the drug, but in no case was an abrupt arrest of the heart witnessed.

(14.3.90.) Cat of 4½ lbs. Etherized—usual preparation. (The animal had already had a 10 cub. centims. bulb of methyl nitrite by inhalation, and two administrations of iso-butyl nitrite $\frac{1}{100}$ cub. centim.) A 9 cub. centims. bulb of methyl nitrite was connected with the femoral vein, and injection gradually made at the time indicated.

The original pressure was 59, the pulse 79, and respiration 59. Tracing 25*a* (slow), tracing 25*b* (fast).

On injection the pressure fell to 21, a momentary pause having occurred at 39 seconds.

In 2 minutes pressure was 15 millims.
" 4 " " 10 "
" 6 ". death.

Tracing 25*a*.

Injection of gaseous methyl nitrite into femoral vein. For pulse see quick cylinder tracing 25*b*.

Tracing 25*b*.

Injection by femoral vein of methyl nitrite (9 cub. centims. bulb). (Reduced one-half.) The lowest line records respiration; the stars indicate duration of injection; the middle line is the pulse and pressure; the top line is continuous with the middle one. Owing to contact of the pens in the lowest pair of lines the respiration is not recorded during the latter part of the tracing. For pressure see tracing 25*a* taken upon slow drum.

	Time.	Pulse.	Respiration.
	secs.		
Before injection . . .	0	79	
Slow injection of gaseous methyl nitrite	15	79	Respiration ceased
	25	80	
	35	87	
	45	89	Three faint respirations
	55	87	
	65	87	
	70	79	
	75	53	
	80	52	
	95	46	
	105	46	Artificial respiration commenced
	135	31	
	155	30	Artificial respiration was maintained 4 minutes, but heart gradually failed and then stopped at 6 minutes after inhalation was begun

It would be injudicious to compare too closely the action of this *gaseous* nitrite administered by injection with that of the other *liquid* nitrites, as the necessary data for the comparison cannot be obtained.

The respiration and heart are both profoundly affected by it in the doses indicated. By inhalation also the drug is very active and has a powerful tendency to arrest respiration. The extent to which it lowers the pressure places it above ethyl nitrite, as its average effect is greater.

The reduction of blood-pressure is often prolonged, as has been recorded in the case of the ethyl compound.

Judging from these inhalations in which the pressure was more or less perfectly recovered, the relative position of methyl nitrite to the other bodies examined may be stated as follows:—Its effect in reducing pressure would place it above butyl nitrite and ethyl nitrite, but below tertiary amyl nitrite and the remaining butyl compounds. It most nearly approaches α-amyl nitrite in this respect. The extent of its action appears to be greater than that of the other compounds owing to its depressant effect on the respiration, and frequently also on the heart.

Methyl nitrite has proved lethal in smaller doses than the other nitrites examined.

V.—GENERAL SUMMARY OF BLOOD-PRESSURE EXPERIMENTS.

The chief result of these experiments may be broadly indicated as follows:—

All the nitrites examined produce, in whatever way administered, a reduction of blood-pressure—variable, however, according to the compound employed, in extent and progress as well as in the ensuing recovery.

Acceleration of the pulse usually accompanies and succeeds the fall of pressure on inhalation, the extent of acceleration varying in the individual nitrites. It may be stated that the acceleration is less upon intra-vascular injection—especially when intra-arterial—than after inhalation. A distinct retardation of the pulse is frequently produced when the injection is into the carotid artery.

The extent of acceleration appears to be less in cats than in the human subject. It is probably also less in cats than in dogs, judging from the experiments on the latter recorded by other observers. (In the experiments of others a mixed nitrite of amyl was employed, and the absence of exact information as to the amount inhaled makes it difficult to compare them with the results now described. The question has not been considered of sufficient importance in the present connection to induce us to enter upon it.)

The respiration is affected by the nitrites (1) temporarily during, and immediately subsequent to, inhalation in various degrees, some of them proving much more active than others. (2) It is affected permanently by the repeated administration of the same or of different nitrites. The action of the nitrites in these respects may be contrasted by arranging them in a tabular form according to their activity.

I. *Reduction of Blood-pressure.*

(*a.*) On inhalation.
(*b.*) On intra-vascular injection.

(*a.*) Greatest effect for similar doses (by volume) of the nitrites enumerated, administered by inhalation—

1. Secondary propyl nitrite.
2. Tertiary butyl „
3. Secondary butyl „ } nearly equal.
4. Iso-butyl „ }
5. Tertiary amyl „
6. α-amyl „ } nearly equal.
7. α- and β-amyl „ }
8. Methyl „
9. Butyl „
10. Ethyl „
11. Propyl „

(*b.*) Greatest effect on intra-vascular (venous) injection.*

1. Secondary butyl nitrite.
2. „ propyl „ } nearly equal.
3. Iso-butyl „ }

---

* Methyl nitrite invariably caused death when administered by injection in the gaseous form, this result being probably due in part to aerial embolism. If the extent of the first fall were only taken

4.	Tertiary butyl	nitrite	nearly equal.
5.	„ amyl	„	
6.	Butyl	„	
7.	α-amyl	„	
8.	α- and β-amyl	„	
9.	Ethyl	„	nearly equal.
10.	Propyl	„	

II. *Longest Duration of Subnormal Pressure* after—

(*a.*) Inhalation of equal quantities by volume of the nitrites.

(*b.*) Intra-vascular injection of equal quantities by volume of the nitrites.

(*a.*) *Inhalation.*

1.	Methyl	nitrite.	
2.	Ethyl	„	
3.	Tertiary amyl	„	nearly equal.
4.	Tertiary butyl	„	
5.	Secondary butyl	„	
6.	Butyl	„	
7.	α-amyl	„	nearly equal.
8.	α- and β-amyl	„	
9.	Iso-butyl	„	
10.	Secondary propyl	„	
11.	Propyl	„	

(*b.*) *Intra-venous Injection.**—The following order may be taken as approximately correct, though the rates of return of pressure have not proved so constant in the case of individual nitrites as was the fall of pressure they produced.

1.	Ethyl	nitrite.	
2.	Tertiary amyl	„	
3.	α-amyl	„	nearly equal.
4.	α- and β-amyl	„	
5.	Secondary propyl	„	
6.	Butyl	„	
7.	Tertiary butyl	„	
8.	Secondary butyl	„	
9.	Propyl	„	nearly equal.
10.	Iso-butyl	„	

---

methyl nitrite would stand before ethyl nitrite, and nearly on an equality with α-amyl nitrite. It has been deemed advisable, however, not to introduce it into the series.

* See note on methyl nitrite administered by injection.

III. *Greatest Acceleration of Pulse* after*—

(*a*.) Inhalation.
(*b*.) Injection of equal volumes of the nitrites.

(*a*.) *Inhalation.*

1. Tertiary amyl nitrite.
2. α-amyl „
3. α- and β-amyl „
4. Tertiary butyl „
5. Iso-butyl „
6. Secondary butyl „
7. Butyl „
8. Secondary propyl „
9. Propyl „
10. Methyl „
11. Ethyl „

(*b*.) *Intra-venous Injection.*†

1. Tertiary amyl nitrite.
2. α-amyl „
3. α- and β-amyl „
4. Tertiary butyl „
5. Secondary butyl „
6. Butyl „
7. Iso-butyl „
8. Secondary propyl „
9. Propyl „
10. Ethyl „

IV. *Action of Nitrites Administered* (A) *by Inhalation on Respiration.*

Amyl Nitrites.—The usual course of the respiration on administering α-amyl nitrite is a slight retardation at the commencement of inhalation, succeeded by an acceleration of 5 to 9 per minute. Frequent administrations tend to cause a lasting retardation. The mixed α and β compounds and the tertiary amyl nitrite cause a very similar effect.

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* It will be understood that when retardation of the pulse is produced in place of acceleration, this is caused chiefly by the bodies towards the end of the series.

† Acceleration only occurs with moderate regularity after the nitrites at the upper end of the series (the first three places). Below this point retardation of the pulse becomes more common until, at the lower end, it is a well-marked phenomenon.

Methyl nitrite, though omitted from the list, causes a retardation before death, which would place it below ethyl if the doubtful character of its action did not render its classification unadvisable.

Butyl Nitrite tends to cause a distinct retardation during inhalation, more marked and lasting than in the case of the amyl compounds, and succeeded by less acceleration.

Iso-Butyl as well as secondary butyl and tertiary butyl nitrites cause a very marked slowing, frequently with a pause in respiration. This slowing may last for some minutes after inhalation, or may yield to an acceleration which is rarely so marked as that produced by the amyl compounds. A deepening of respiration follows the early retardation of pause.

Propyl Nitrites do not affect the respiration so much as the butyl compounds. They may produce a little slowing at first, or the respiration may remain unaltered till 30 to 40 seconds after inhalation has commenced, when some acceleration usually results, but this acceleration is more marked after the amyl compounds. The secondary propyl nitrite produces a stronger effect than the primary.

Ethyl Nitrite, in doses which materially reduce the blood-pressure, causes a marked slowing with an occasional tendency to pause. This retardation may last for some time, the respiration becoming somewhat deeper, or it may ultimately yield to a limited acceleration.

Methyl Nitrite acts powerfully in retarding the respiration, and in tending to produce a pause which is often prolonged in character. The respiratory effort appears distinctly weakened by the nitrite, even in absence of the slight degree of acceleration which may occasionally be observed. The gaseous methyl nitrite is probably the most active member of the series in this respect.

Action of Nitrites Administered (B) *by Intra-vascular Injection on Respiration.**

Modification of respiration by the various nitrites is not so readily produced by injection as by inhalation.

The Amyl Nitrites cause an acceleration of 2 to 4 respirations per minute throughout, or exceptionally cause a retardation of 2 or 3 as a preliminary to the acceleration.

The Butyl Nitrites do not produce the initial pause which so frequently follows upon their inhalation, but they occasion a marked slowing of respiration, which usually lasts for 2 minutes, after which it returns to the normal rate, or slightly exceeds it. The tertiary butyl nitrite appears to be most active of the four in causing this alteration.

The Propyl Nitrites influence the respiration but little, a slight acceleration of 3 per minute, and lasting for 90 seconds, is usual after the secondary nitrite. The primary in the doses of $\frac{1}{100}$ to $\frac{1}{50}$ cub. centim. frequently produces no change beyond a retardation or acceleration of 1 per minute.

Ethyl Nitrite.—Considerable slowing of respiration follows the injection of $\frac{1}{18}$ cub. centim. which may amount to 60 per cent. or more of the respirations, and often persists for some minutes. A smaller dose ($\frac{1}{38}$ cub. centim.) produces a distinct retardation.

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* This general statement is submitted in place of the details in the notes of experiments, which it was concluded not to burden with records of slight respiratory changes caused by injection.

Methyl Nitrite renders the respiration irregular and gasping, in 60 seconds the respiratory movement has become faint, and ceases altogether about the time that the heart stops.

The Ethyl and Methyl Nitrites produce a more marked effect on respiration than any other members of the series.

We postpone the consideration of the cause of divergences in the effects produced by the various nitrites to the end of the paper, where they will be discussed in connection with the chemical constitution of these bodies.

VI.—GENERAL CONSIDERATION OF THE MODIFICATION OF NITRITE ACTION BY SPLANCHNIC STIMULATION AND SECTION.

The influence of the various nitrites has been studied with the sympathetic nervous system intact; it has also been tested after both splanchnic nerves in the cat had been divided, and during their subsequent stimulation. The complicated nature of the experiment made it difficult to reproduce exactly the conditions of pressure, &c., which would be necessary for an exact comparison of the long series of nitrites examined, attention will therefore be directed to the more general effects produced by these bodies and only the broader distinctions recognisable between them will be indicated.

Division of the splanchnic nerves is attended by a considerable fall of blood-pressure, from this fall of pressure a temporary and partial recovery may, however, occur, and it is clear that there are still agencies in play besides the part capable of modifying the general pressure to a considerable extent. After splanchnectomy all the organic nitrites are capable of causing a still further fall of pressure, though their effect is not so great as before section.

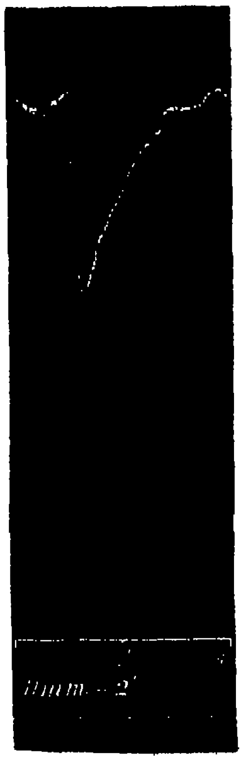
Apart from the peripheral ganglionic plexuses, which, according to some observers, may possibly preserve a certain degree of control after double splanchnectomy, it would be both remarkable and anomalous if changes in the composition of the blood were incapable of producing any alteration upon the relaxed walls of the vessels.

We have no reason for asserting that the dilatation after section of the sympathetic is exactly equivalent to nitrite dilatation. The former is probably not a maximal dilatation, for LUDWIG and CYON found that when they stimulated the depressor nerve after section of both splanchnics the blood-pressure fell still further. It is very possible that the fall of pressure after nitrite inhalation is attributable to changes in the splanchnic area, in addition to the dilatation which undoubtedly occurs in other areas. BRUNTON found that after section of the cervical cord a reduction of pressure still took place on nitrite inhalation.

If during the continuance of pressure-reduction which follows splanchnectomy the nitrites are administered, the fall, though occurring, is not equal to its previous extent. If, on the other hand, the nitrite is given during one of the temporary spontaneous elevations which from time to time occur, a fall closely approaching the original is recorded.

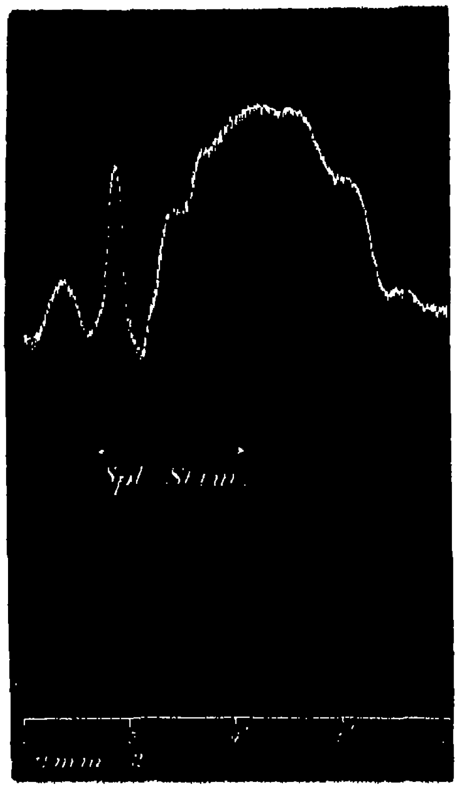
The following experiment will serve for purposes of contrast.

Tracing 26*a*.



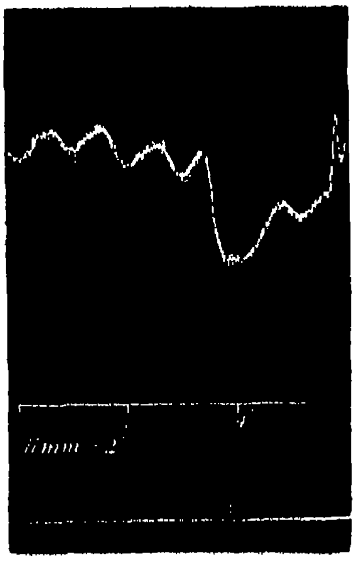
Both splanchnic nerves divided. Inhalation of $\frac{1}{100}$ cub. centim. secondary propyl nitrite.

Tracing 26*b*.



Stimulation of splanchnic, coil 7·5 centims., and simultaneous administration of $\frac{1}{100}$ cub. centim. secondary propyl nitrite.

Tracing 26*c*.



Taken 30 minutes after 26*b*. During occurrences of TRAUBE's curves administer $\frac{1}{100}$ cub. centim. secondary propyl nitrite.

Experiment.—Cat slightly curarised and steadily etherized. Administration of $\frac{1}{100}$ cub. centim. secondary propyl nitrite. Splanchnics intact. Fall of pressure 44 millims., recovered in two minutes. After splanchnectomy the same administration during a temporary rise of pressure (viz., a rise from 85 to 118 millims.) caused a fall of 39 millims., recovered in 140 seconds (tracing 26*a*). The pressure having fallen again to, and somewhat below, the original level after splanchnectomy, the splanchnic was stimulated by a current (coil 7·5 centims.) just bearable to the tongue (tracing 26*b*), the $\frac{1}{100}$ cub. centim. of secondary propyl nitrites being given at the same time. A rise of pressure of 35 millims. succeeded by a fall of 39 millims. was recorded, as contrasted with 39 millims. from the previous experiment; but the subsequent recovery was more rapid, occurring under the continued splanchnic stimulation—to the normal in 93 seconds—and passing beyond it to 120 millims.

It is worthy of note that the pressure does not fall at once on discontinuing splanchnic stimulation, but outlasts it for 140 seconds and then gradually declines to the previous level. Half an hour subsequent to the administration the pressure had fallen to 66–7, fluctuation recorded as long waves being present. Secondary propyl nitrite in the original dose (tracing 26*c*) reduced this pressure slowly by 20 millims. The pressure rose in 2 minutes 30 seconds to the normal and passed beyond it.

From a consideration of these curves, it appears—(1) that the constriction of arterioles in the vascular area supplied by the splanchnic may be restored spontaneously and temporarily to some extent, after both nerves have been divided, and then abolished by secondary propyl nitrite.

(2) That the increased pressure resulting from splanchnic stimulation may be reduced by administration of nitrite, but that after recovery of pressure an increased tonus of the vessels may remain for a considerable time.

(3) That when no spontaneous temporary elevation of pressure is present after double splanchnectomy, a reduction of the existing pressure by the nitrite still occurs.

As a corollary to the fact already stated, that such bodies as the secondary propyl, iso-butyl, secondary and tertiary butyl nitrites have proved themselves the most active members of the series of organic nitrites examined in their action upon blood-pressure—the splanchnics being intact—it was found that these prove themselves specially capable of cancelling the rise of pressure which would usually be produced by a given splanchnic stimulation.

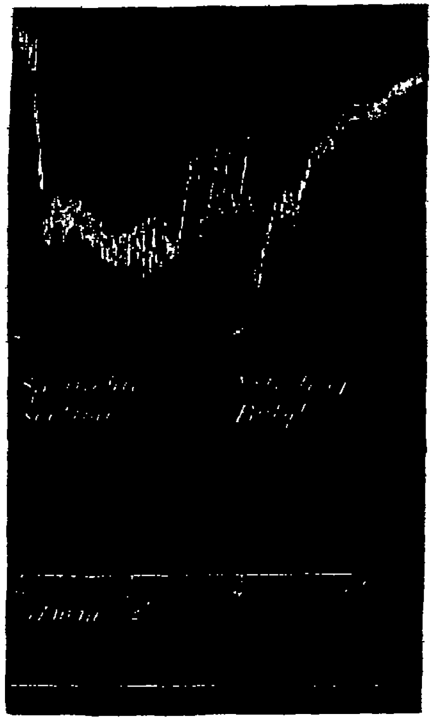
After double splanchnectomy a marked resistance to nitrite effect has been observed during the occurrence of extensive waves of changing pressure, as evidenced by the rapid rise of pressure after the nitrite fall. This effect is indicated by a tracing taken from an experiment in which the splanchnics had just been divided.

At the time shortly before nitrite inhalation the pressure, which was fluctuating between 95 and 82, described four waves having a variation of from 110 to 93 millims. (tracings 27*a* and 27*b*.)

On giving the butyl nitrite $\frac{1}{50}$ cub. centim. the pressure fell from 110 to 79, but 1 minute after commencing, or, in other words, when the summit of the wave which would have followed the other four in regular series was approached, there was a distinct rise. In so short a time as 82 seconds the normal pressure was reached, and thereafter exceeded, the waves gradually disappearing.

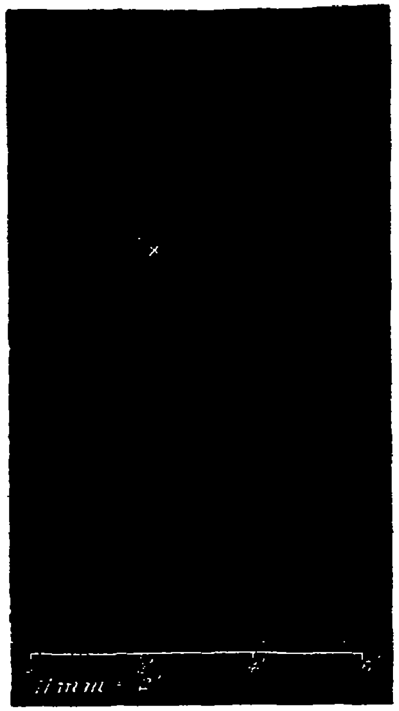
	Time.	Pulse.
	secs.	
Before inhalation . . .	..	136
After commencement .	5	140
,, ,, .	25	140
,, ,, .	45	142
,, ,, .	60	142
,, ,, .	85	144
,, ,, .	105	141
,, ,, .	130	139

Tracing 27*a*.



nhalation of $\frac{1}{50}$ cub. centim. butyl nitrite four m ıtes after division of splanchnic nerves. The nitrite fall followed by a rapid rise of pressure. The pulse is sho n in 27*b* recorded upon a rapidly moving cylinder.

Tracing 28*a*



Stimulation of splanchnic nerve (coil 2·5 centims.) and simultaneous inhalation of $\frac{1}{36}$ cub. centim amyl nitrite. For pulse see tracing 28*b*.

Tra ing 27*b*.

ıhalation of butyl nitrite $\frac{1}{30}$ cub. centim. after section of both splanchnic nerves. Reduced one-half. The top line shows pulse and pressure, the lowe the signal record of the time of administration. See also slow record of pressure, tracing 27*a*.

Tracing 28*b*.

Stimulation of splanchnic nerve accompanying adı inistration of amyl nit ;e. Reduced one ıalf Th upp r line show u se and , the lower the signal record of adminis ation and stimulation. For course of blood-pr ur slow drum, tr 28*a*.

Before this administration there appeared to be an unusual vasomotor excitement, which offered some degree of resistance to the nitrite effect.

After dilatation of the vessels had been increased by nitrite, an unusual contraction appears to succeed, as in some of the experiments just recorded. In this instance pressure rises to within 12 millims. of the point at which it stood before splanchnectomy.

It is necessary now to examine somewhat more closely the results of splanchnic stimulation at various periods of nitrite activity. The former may be considered under three headings with regard to the latter. Splanchnic effect occurring—

1. Before inhalation, or during the initial stage of inhalation, anterior to the fall;
2. During the period of fall of pressure; or
3. During a time at which a rise of pressure usually occurs.

If the inhalation of one of the nitrites is made simultaneously with the admission of a strong faradic current to one splanchnic (the companion having been previously divided), a rise of blood-pressure is at once observable. This elevation commences within 3 seconds after the stimulation is begun, and attains its maximum in about 8 to 10 seconds, some variations occurring according to the strength of the current and to the activity of the nitrite given.

Although stimulation is still continued, a distinct and steady fall of pressure commences, the fall at this point coming into contrast with that usually following a simple inhalation, as it shows a nearly equal decline for similar increments of time; whereas after inhalation, as has been already shown, the decline is much greater at first, and thereafter proceeds gradually. The loss of control of the splanchnic is gradual and not sudden. The minimal point of pressure is reached at a time distinctly after that at which it usually occurs, nevertheless a fall to a point below the original pressure level is uniform.

Usual preparation of animal; artificial respiration; both splanchnics divided, the left nerve on electrodes. (Tracings 28*a* and 28*b*.)

Time.	Blood-pressure.	Pulse.	
secs.	millims.		
0	84	168	Before administration splanchnic stimulated coil 2·5, and administered $\frac{1}{36}$ cub. centim. mixed α and β-amyl nitrite
5·5	108	166	
22·5	89	. .	Splanchnic stimulation off
26	84	171	
42	62	. .	Pressure at lowest and beginning to rise
131	84	. .	Pressure normal and rising rapidly
218	95		

This fact is of special significance when it is borne in mind that the powerful closure of the mesenteric and visceral vessels, which the splanchnic stimulation provokes when administration and stimulation are simultaneous, reduces the free passage of the blood laden with nitrite vapour to the arterioles, and, therefore, must limit the local effect which the drug is capable of producing. It is difficult to see what satisfactory explanation can be given by the advocates of an exclusively central cause of the fall of pressure which occurs during simultaneous nitrite inhalation and splanchnic stimulation, unless they recognise a vascular area more capacious than that dominated by the splanchnic, and beyond its control, which is relaxed by such a central effect. If a less capacious area were relaxed, the splanchnic territory being unimpaired in activity, stimulation of the latter ought clearly to obviate the nitrite fall produced elsewhere.

The initial rise occurring from stimulation of the splanchnic at the same time that nitrite was given is succeeded by a fall, whilst the stimulation is maintained; there is, therefore, an instant during which the original level of blood pressure is crossed as the decline progresses.

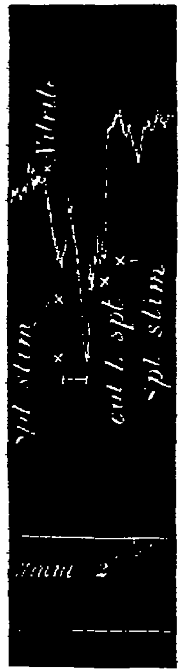
This point occurs in from 25 to 30 seconds after the commencement of administration, or, in other words, about the time of greatest nitrite effect for the doses of nitrite used, the splanchnic being unstimulated.

If we imagine all other vascular areas which are usually influenced by nitrite action to be in their condition of maximal dilatation for a given dose at this time, we should expect the usual rapid recovery of pressure to result at this point, if the action of the nitrite were central from the return of activity to the vasomotor centres, but this effect is very rarely witnessed. The pressure is in part falling from a progressive weakening of splanchnic control upon the vessels, to which, as they dilate, more of the nitrite-laden blood has access. In this way a later maximum of dilatation is brought about.

2. If the nitrite administration precedes splanchnic stimulation by such a time interval as admits of the former having caused about half the reduction of pressure of which it is capable (*i.e.*, about 15 seconds after the commencement of inhalation), then the controlling action of the splanchnic is still further reduced, and an immediate rise to the original pressure by stimulation of physiological or somewhat greater strength is not met with, although a slight effect may be produced according to circumstances. How slight this effect actually is may be seen from the following experiment; the fall of pressure was less by 5 millims. than that occurring from the same dose of the same nitrite in the absence of splanchnic stimulation.

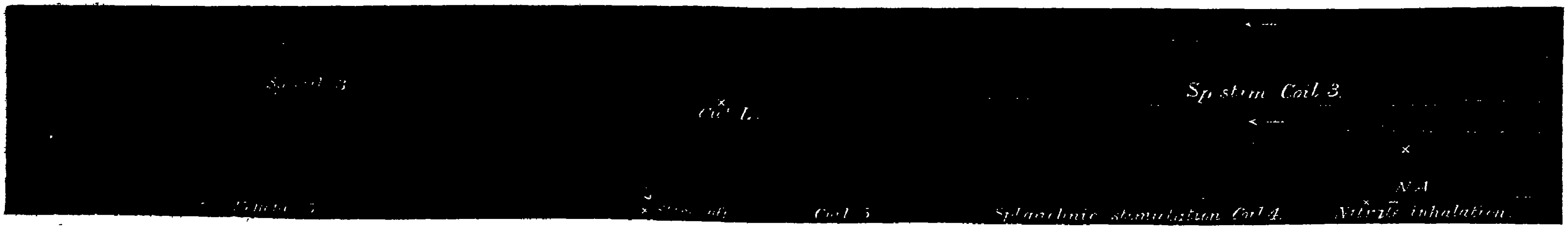
Experiment.—Usual preparation. Right splanchnic divided and placed on electrodes. Left splanchnic intact. Artificial respiration. (Tracings 29*a* and 29*b*.)

Tracing 29*a*



Inhalation of $\frac{1}{42}$ cub. centim. amyl nitrite 15 seconds before right splanchnic stimulation. During progress of rise of pressure the other splanchnic nerve is divided, causing arrest of rise. Stimulation of right splanchnic causes great and sustained rise. For pulse see tracing 29*b*.

Tracing 29*b*.



Stimulation of splanchnic nerve following administration of amyl nitrite. Reduced one-half. The lower pair of lines show pulse and the signal record, the upper are continuous with them. For course of blood-pressure see slow cylinder, tracing 29*a*.

Time.	Blood pressure.	Pulse.	
secs.			
0	91	168	
15	76	171	Gave $\frac{1}{48}$ cub. centim. mixed amyl nitrite. (III.)
20	85	174	Splanchnic stimulation coil, 4 centims. and pushed up to 3
36	56		
47	55	..	Lowest pressure
48	..	..	Began to rise
72	76	170	
82	..	..	Stimulation splanchnic coil 3
96	..	..	Stimulation stopped
100	104	170	
120	..	..	Cut left splanchnic
125	96		
140	..	..	Stimulated right splanchnic
148	112	180	

But it may be argued that the stimulation in this case was not continued throughout the nitrite action, and that some controlling effect upon the fall was therefore not recorded. Curves have, however, been frequently obtained in which stimulation was continued fully 1 minute after inhalation commenced, and yet the fall of pressure recorded was within a few millimetres of that obtained in the absence of splanchnic stimulation, although the subsequent rise after the minimum pressure had been reached was rapid.

This effect was especially well marked in the case of iso-butyl nitrite, which, in a given dose, throws the splanchnic more completely out of action than pure nitrite of amyl does.

After the pressure had recovered in these cases the splanchnic was usually tested, in order to ascertain that it still responded; and it was invariably found that a prompt and considerable rise of pressure resulted. It was noticed that late in the course of an experiment, after the pressure had been reduced by double splanchnectomy, and to an additional extent by administering a nitrite, the prolonged depression apt to result could be obviated by stimulating the splanchnic, and that the pressure could even be "pushed up" and retained at a relatively high level by repeating the stimulation at intervals. After nitrite inhalations, succeeding double splanchnectomy, the pressure is frequently seen to rise spontaneously to a higher level than before the administration, and to remain elevated for a considerable time. Whether this is the result of an increased potentiality for contraction of vascular areas after their dilatation is at present difficult to decide, but it seems not improbable that this may be the explanation of the phenomenon.

(3.) Of splanchnic stimulation occurring at the time of commencing recovery of pressure after nitrite action, it is only necessary to say that it markedly accelerates the return of the pressure to, and even beyond, its original level.

VII.—Action of Nitrites upon the Human Subject.

It has been already mentioned that these experiments were confined to obtaining an accurate record of pulse rate, and to noting the various subjective and objective symptoms to which the nitrites give rise.

Inhalation in all cases took place by means of a mask inhaler which was specially constructed by Messrs. Maw, Son, and Thompson.

This consists of a somewhat conical metal box covering the mouth, and fitting accurately over the bridge of the nose by means of a hollow rubber border which could be distended by injection of air. It was provided with three tubes opening out of a common trunk in the front of the mask; one of these had no valve, but the two lateral tubes had each one valve, opening inwards and outwards respectively.

The tube intended for the inspiration of the nitrite had a continuation of india-rubber, in the middle of which a glass bulb was inserted for the reception of the nitrite. Spring clamps were placed on each side of this bulb.

For accurate comparison the results of administering the nitrite to the *same individual,* and usually on the *same day* are contrasted. There is considerable variation in different individuals to nitrite effect. In a distinctly neurotic subject, in whom the prospect of the inhalation alone was apt to cause a marked pulse acceleration, a dose of $\frac{1}{36}$ cub. centim. (= ·023 grm.; NO_2 0·009 grm.) of pure amyl nitrite, increased the rapidity of the pulse (from 77 to 136), the acceleration being accompanied by a very perceptible subjective and objective nitrite effect, but there was afterwards a rapid fall nearly to the normal. In a second subject of a lymphatic tendency the increase of pulse-rate was by no means great, but it was remarkable as being continued much longer than in other subjects of experiment.

The mask having been adjusted to the face, and respiration being regular through the valveless tube, the drum was started at full speed to record the normal pulse-rate,* and the inhalation tube was opened by removing the clamps on each side of the bulb, at the same time that the anterior tube was closed. The time of inhalation was recorded by a signal marker which was under the exclusive care of one assistant, while another assistant watched the face and neck for indications of flushing or other appearances.

Several Aberdeen students kindly gave their assistance in these experiments amongst whom were Messrs. Ettles (who also sketched the apparatus employed), Lendrum, Sutherland, and Taylor.

It is not intended to devote much space to the description of the results obtained, but rather to present them in summarised form.

The nitrites examined were various specimens of: pure α-amyl nitrite; the three mixed α and β-amyl nitrites, designated I., II., and III.; butyl and iso-butyl nitrites; primary and secondary propyl nitrites; and ethyl nitrite.

---

* The impulse was derived from the cardiac apex, or radial artery, and transmitted to a Marey's recording tambour.

The doses of nitrite employed varied from $\frac{1}{42}$ to $\frac{1}{18}$ cub. centim. Doses of $\frac{1}{18}$ cub. centim. of amyl nitrite caused an acceleration of the pulse, commencing at the end of the first 5 seconds. The acceleration was equivalent to from 65 to 73 per cent. of the pulse rate. Retardation of the pulse during the early stage of administration was not observed. Although the acceleration began between the fifth and tenth seconds, it was from the tenth to the thirtieth that the more rapid increase occurred, the acceleration reaching its maximum somewhat later, viz., at the thirty-fifth second.

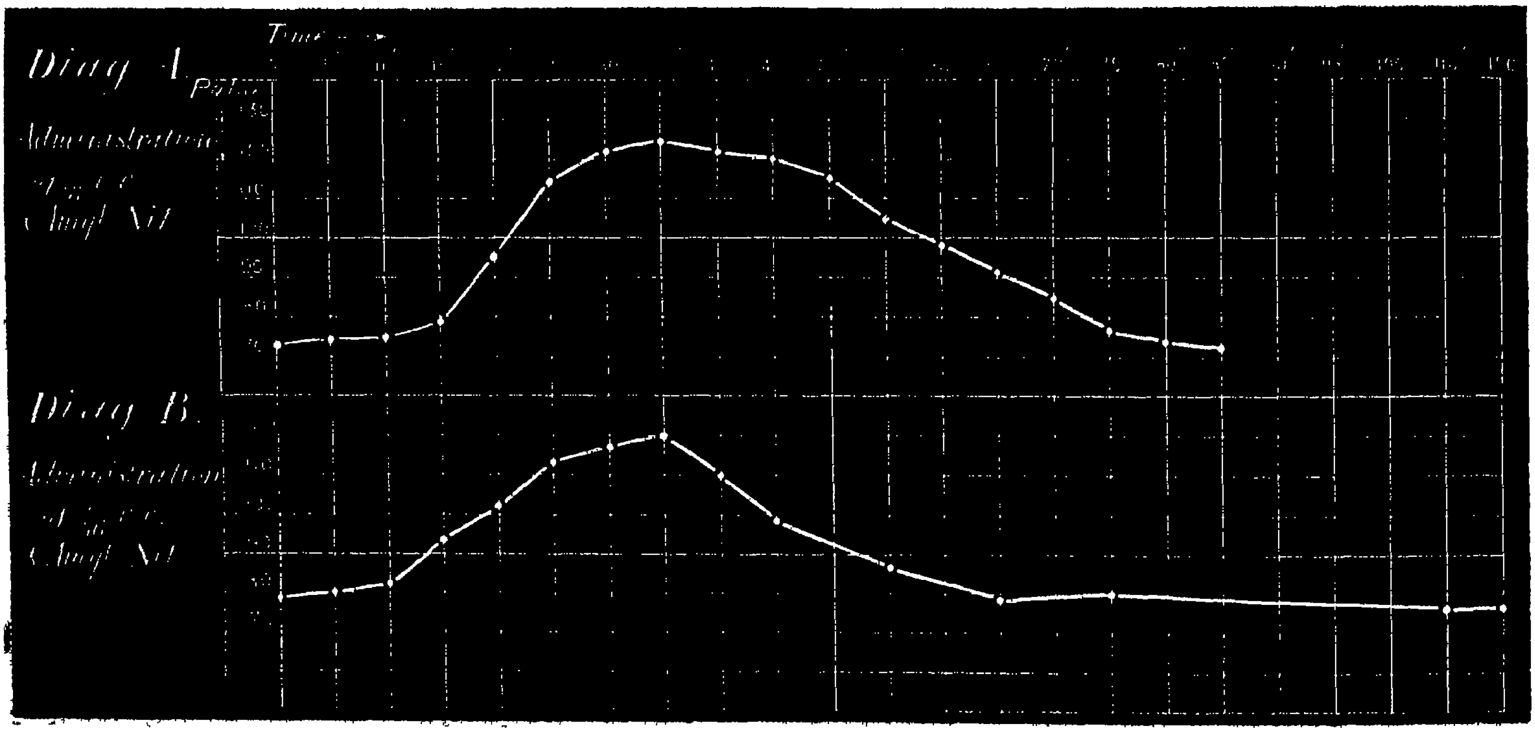
If divided into three periods of 10, 10, and 15 seconds respectively, the percentage of the total acceleration, amounting to 45 to 50 beats, averaged about as follows:—

1st 10 seconds = 6 per cent.
2nd 10 " = 40 "
Last 15 " = 54 "

After the maximal acceleration is reached a fall begins somewhat gradually, the pulse returning to its normal within 90 seconds after inhalation commenced. The fall is trivial from the 35th to the 45th second; from the 45th to the 65th second it is most rapid, and then declines more gradually. Fall in successive 10 seconds after maximal acceleration:—

1st 10 seconds = 10 per cent.
2nd " = 30 "
3rd " = 33 "
4th " = 27 "

Diagrams A and B.



Experiment. Diagram A.—Administration of $\frac{1}{18}$ cub. centim. α-amyl nitrite to T. Ordinates which are united at their summits to form a curve represent intervals of 5 seconds.

T. afterwards stated that the pulsation was violent in his head and carotids; there was slight vertigo. The flushing was very well marked and more lasting than when $\frac{1}{36}$ cub. centim. was given.

	Time.	Pulse.
	secs.	
Pulse before nitrite . .	0	73
Inhalation commenced .	5	74
	10	76
	15	79
	20	95
	25	115
	30	122
	35	125
	40	122
	45	120
	50	116
	55	108
	60	99
	65	91
	70	85
	75	77
	80	73
	85	72

A dose of $\frac{1}{36}$ cub. centim. caused an acceleration of 35 to 40 beats per minute (equal to from 47 to 53 per cent. of the total). The pulse occasionally showed a slight slowing during the second 5 seconds of inhalation; more usually there is acceleration. The maximal acceleration was from 25 to 30 seconds after inhalation commenced, the latter being much the more frequent.

The pulse returned to the normal in from 55 to 60 seconds, and then frequently became distinctly subnormal for a short time.

The relationship of rise and fall may be briefly indicated by the percentage acceleration and reduction of pulse.

secs.	per cent.	
0 to 10	7	Pulse accelerating.
10 ,, 20	52	
20 ,, 35	41	
35 ,, 45	51	Pulse slowing.
45 ,, 55	30	
55 ,, 65	19	

The figures in these two experiments indicate a later maximal effect, a greater and more prolonged acceleration, and a more gradual decline after the larger than after the smaller dose.

Experiment. Diagram B.—Administration of $\frac{1}{30}$ cub. centim. amyl nitrite.

T. afterwards described his sensations as of active pulsation in head and neck, unaccompanied by dyspnœa. There was no vertigo. The flushing was very well marked, but not of long duration.

	Time.	Pulse.
	secs.	
Pulse before nitrite . .	0	79
Inhalation commenced .	5	80
	10	82
	15	94
	20	103
	25	114
	30	118
	35	120
	40	110
	45	99
	55	87
	65	79
	80	80
	105	75
	120	75

Variations from the Normal α-Amyl Nitrite Effect caused by the Various Organic Nitrites Examined.

The three mixed α- and β-amyl nitrites (I., II., and III.) were administered by inhalation in addition to pure α-amyl nitrite. The action of the four bodies was very similar, that is to say, they caused, for the dose administered, a powerful acceleration of the pulse, and the rate at which the acceleration progressed and receded was nearly the same. If a distinction is justifiable between them, it must be based on a somewhat more powerful action of pure amyl nitrite and the compound I. when compared with II. and III. In the course of three experiments devoted to the comparison of these bodies, and performed on different subjects, it was found that the variation in the pulse-rate in all of them was not greater than four beats per minute for the $\frac{1}{36}$ cub. centim.

The maximal acceleration after doses of $\frac{1}{36}$ cub. centim. is usually from the 28th to the 35th second after the beginning of inhalation, the pulse usually falling to the normal in 60 seconds to 65 seconds. It is usual to witness a temporary subsequent decline in pulse-rate amounting to two beats to three beats below that antecedent to inhalation.

Primary Butyl Nitrite.

In experiments with this compound made on carnivorous animals, the acceleration of the pulse was less marked than in contrast experiments with amyl compounds.

The relationship of the acceleration caused by butyl nitrite to that of amyl nitrite may be represented by percentages taken from three individuals.

T. Butyl nitrite caused an acceleration of 79 per cent. of that produced by α-amyl nitrite.
S. ,, ,, ,, 75 ,, ,, ,,
L. ,, ,, ,, 74 ,, ,, ,,

The maximal acceleration is soon arrived at. It lies between the 25 seconds and 28 seconds after commencing inhalation for the dose of $\frac{1}{36}$ cub. centim.

The return to the normal pulse-rate was usually 3 seconds to 5 seconds earlier than it was after the inhalation of amyl compounds. The subjective symptoms were not so well marked.

Experiment 3, L.—Inhalation of $\frac{1}{36}$ cub. centim. butyl nitrite.

Throbbing in thyroid and carotid regions; pulsation at occiput; felt flushing in face. Afterwards received same amount of mixed amyl nitrite (II.) and flushed more, stating afterwards that he felt pulsation and warmth of surface distinctly greater than during administration of butyl nitrite. The pulse after (II.) showed a greater acceleration.

Iso-Butyl and Secondary Butyl Nitrites.

Both of these bodies cause less acceleration of the pulse than the amyl compounds, but greater than that produced by butyl nitrite. The acceleration occasioned by the secondary butyl nitrite (about 80 per cent. of that produced by α-amyl nitrite) seems to be slightly less than by the iso-butyl compound (about 82 per cent.). The greatest acceleration produced by both of them seems to occur between the 25th and 30th seconds. The subjective symptoms after $\frac{1}{36}$ cub. centim. are further more marked in the case of secondary butyl nitrite; after both of them the characteristic flushing and throbbing are produced by even this small dose.

The duration of pulse acceleration after either of them is shorter by a few seconds than after a corresponding dose (by volume) of α-amyl nitrite.

Primary and Secondary Propyl Nitrite.

Both of these bodies come after butyl nitrite in activity, but of the two, secondary propyl nitrite causes distinctly greater acceleration of the pulse.

For comparison, they may be averaged in doses of $\frac{1}{36}$ cub. centim. with pure α-amyl nitrite, which has the value of cent. per cent.

L. { Primary propyl nitrite 62 per cent.
Secondary ,, 76 ,,

This slight acceleration is early developed and rapidly reduced, a reduction to the normal pulse-rate being reached sooner than with pure amyl nitrite given in an equal dose.

This is specially the case with primary propyl nitrite, which frequently causes an oscillation of pulse-rate, the first acceleration and its rapid reduction being succeeded by a second feeble acceleration.

Ethyl Nitrite.

Given in the most cautious manner, so that the danger of loss is reduced to a minimum, the effects of small doses are almost nil. An ordinary inspiration, or, at most two, volatilizes the whole of such quantities as $\frac{1}{36}$ and $\frac{1}{30}$ cub. centim. A slight feeling of warmth, and a sweetish taste in the mouth are the only sensations.

The acceleration of the pulse is absent or amounts to only two or three beats in 20 seconds after opening the nitrite tube (E. $\frac{1}{36}$ and $\frac{1}{30}$ cub. centim.); the pulse appears to have a distinct tendency to become subnormal after inhalation.

If the $\frac{1}{20}$ cub. centim. be given, an undoubted acceleration of 10, or even 15 beats per minute is recorded, the maximum is from 25 to 30 seconds after administration is begun.

If a decided impression is thus made upon the pulse-rate, a slight acceleration frequently persists for a time, so that it may be 60 to 70 seconds before the reduction to, or below the original rate occurs.

As regards their power of accelerating the pulse, the substances examined may be thus classified, beginning with the strongest :—

(1.) α-Amyl nitrite.
β-Amyl nitrite.
Iso-butyl nitrite.
Secondary butyl nitrite.
Butyl nitrite.
Secondary propyl nitrite.
Primary propyl nitrite.
Ethyl nitrite.

PART II.

VIII.—ACTION OF NITRITES ON STRIATED MUSCULAR TISSUE.

Nitrite of amyl is well known to possess a powerful action upon the skeletal muscle of Frogs. **WOOD** pointed out that whether applied in a liquid or concentrated gaseous form a paralysant effect was produced. **BRUNTON** speaks of amyl nitrite as a muscle poison in common with all other nitrites. **PICK** also noticed its paralysant action. As we desired to employ a comparatively simple tissue in further contrast experiments upon the nitrites, and as Frog's muscle seemed to fulfil this condition, we instituted the following inquiry into the direct action of the vapours of nitrites upon the muscles of *Rana temporaria.* The paralysant action of nitrite is seldom well developed in instances in which the drug has been administered by injection, no doubt from the fact that the heart's activity is apt to be much depressed before there has been sufficient access of nitrite blood to the muscular system to produce a marked effect upon its irritability. All the experiments in this series were made with the triceps (extensor of the leg) and gastrocnemius of *Rana temporaria.* One of the selected pair of muscles was introduced into a muscle chamber which, whilst being absolutely air-tight, admitted of a connection between the muscle and lever for recording purposes. This chamber, which had a capacity of 50 cub. centims., was a modification of the one described by one of us (C.) in vol. 184, 'Phil. Trans.;' it was closed hermetically above by an india-rubber stopper fitting perfectly air-tight; whilst the opening through which the thread passes to the lever was closed below by a little mercury. The thread works without friction. Stimulation is effected by passing a single opening induction shock from the electrode in contact with the femur clamp, to the tendo Achillis, by means of a fine wire attached to the hook inserted into the latter (see fig. 3). The nitrite was introduced by passing the capillary pipette containing it through a small tube luted into the side of the chamber, having a continuation of india-rubber provided with a screw clamp; the introduction of a small fraction of a drop of distilled water into the tube behind the nitrite, as a preliminary, ensured the complete emptying of the nitrite contained in the tube by displacement, on blowing gently through it with a pair of hand bellows. No escape was possible from the chamber; the fact that the characteristic odour of the nitrite was not recognizable in its vicinity, and further that when the cork was removed, frequently after an interval of more than two hours, the odour of the drug was still distinct within the chamber, showed that the precautions for preventing an escape were satisfactory in their operation. The amounts of the nitrites introduced into the chamber varied from $\frac{1}{30}$ to $\frac{1}{400}$ cub. centim. The second muscle for the control experiment was kept at a like temperature under filter paper moistened with normal salt solution.

Although no difference in the reaction of the second muscle owing to the delay in its examination seemed probable, nevertheless in different experiments the order of examination of two contrasted nitrites was reversed, but the results in the two cases were found to be perfectly uniform. A very extensive series of experiments was necessary, as it is impossible to contrast the gastrocnemius of one Frog with that of another without the possibility of introducing error; and so every member of the series had to be contrasted with each of the other members upon the companion gastrocnemii of the same animals. Each experiment was repeated for the sake of certainty at least thrice, and in many cases five or six times. When the effect of the drug in causing passive shortening and rigor was under consideration the nitrite was introduced after the muscle had ceased to extend under the slight axial weight (5 to 20 grms.) with which it was burdened. When the effect upon the work done was to be considered, a maximal opening stimulation was admitted periodically. The closing stimulation occurring midway between two opening shocks. The closing stimulation was, however, frequently cut out. The speed of rotation of the drums employed was once or four times in an hour.

Fig. 3.

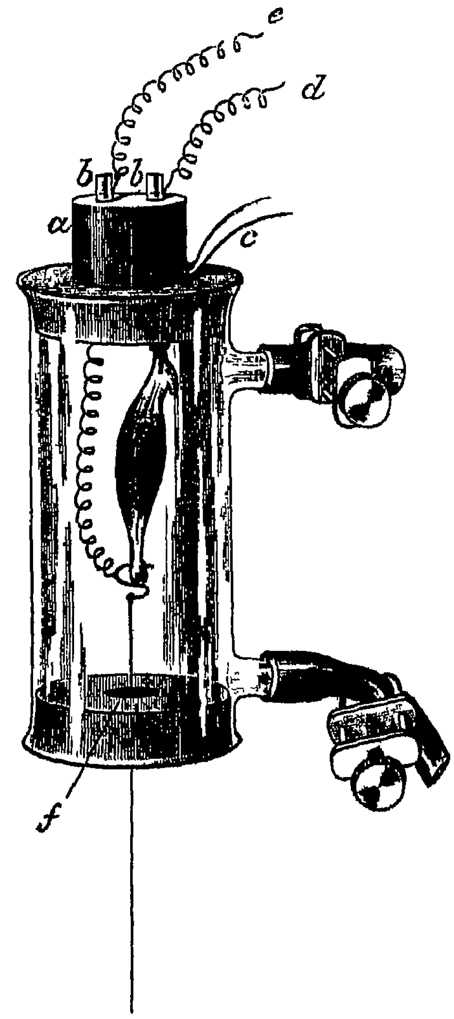


Figure (two-thirds of size) of the air-tight muscle-chamber used in the nitrite experiments.

(The metal band connecting the chamber with the upright as well as the lever are not represented in the sketch.)

The stopper (*a*) which fits air-tight into the opening in the cork at the upper end of the chamber has a double perforation. Both of the openings are closed at their upper ends by glass rods (*b*). The femur is introduced into the lower end of one of these openings and held tightly by a loop of thread, the continuations of which pierce the stopper laterally, so that by traction upon them the bone is clamped in position; these threads are prevented slipping by the pressure of the stopper against the cork rim (*c*). A wire electrode is carried down the side of each glass rod, one of these (*d*) being in connection with the femur round which it is wound, the second (*e*) through the medium of a fine coiled wire with the hook which pierces the tendon. This hook is connected with the lever by a thin silk thread which passes through a fine capillary tube with an hour-glass constriction perforating the bottom of the cylinder. The floor of the cylinder is cupped round the tube so as to afford lodgment to a little mercury (*f*), which renders the chamber perfectly air-tight. The capacity of the closed cylinder was 50 cub. centims.

It is satisfactory to be able to record that the series eventually obtained proved a regular and reliable one with the occurrence of only an insignificant percentage of exceptions, that is to say, if in contrasting the action of nitrites "*a*" and "*b*" on two companion gastrocnemii, "*a*" was found to have the stronger action; and, if contrasting "*b*" and "*c*," the effect of "*b*" was greater, "*a*" was found almost without exception to be distinctly more active, and stronger than "*c*."

After having examined the action of α-amyl nitrite on striated muscle the consideration was entered upon of other amyl compounds containing a known quantity of β-amyl nitrite in addition to α-amyl nitrite; and, further, of the other alkyl nitrite, which have been discussed with reference to their action upon blood-pressure.

Amyl Nitrite.

It will be seen, when the relative activity of the other nitrites upon muscle is described, that the pure amyl nitrite is one of the weaker members of the series. The effects occasioned by introducing accurately measured quantities of α-amyl nitrite into the air-tight chamber containing a Frog's muscle were as follows :—

The $\frac{1}{100}$ cub. centim. (0·0088 grm.; NO_2 = 0·00346 grm.) employed in this manner produces a very marked effect, both when the muscle is (*a*) unstimulated, and (*b*) stimulated.

(*a.*) *Unstimulated.*—No effect is observed for the first few minutes, then a faint tendency to contraction, succeeded by a much more distinct and rapid shortening of the muscle, becomes apparent. The shortening, which is due to the gradual passage of the muscle into rigor, continues for a considerable time (often over 2 hours) before its maximum is reached. The higher the temperature of the cylinder the more rapid the effect of the drug; therefore the two companion muscles of the same animal were necessarily examined under as nearly identical conditions of temperature as possible.

The following figures may be taken as illustrative of the action of pure α-amyl nitrite upon muscle :—

Fresh curarized gastrocnemius in air-tight chamber. Temperature 14° C. Admit $\frac{1}{100}$ cub. centim. pure amyl nitrite. Lever multiplies seven times. Weight, 7·5 grms. (axial).

7 minutes 15 seconds. No alteration hitherto, but here commencement of contraction.

Shortening of muscle.	Elevation of lever.
mins.	millims. (lever × 7)
14	9·5
23	15
40	21
60	28·5
120	40
180	47
240	47·5

(This is the limit of rigor caused. The muscle is hard, white, and contracted.)

In another experiment, temperature 14°·5 C., the initial contraction occurs in 10 minutes 40 seconds.

In a third, temperature 15° C., occurs in 6 minutes 5 seconds.

In a fourth, „ „ „ 3 „ 38 „ .

These figures will give an idea of the possible variations from the same dose, the variations being due partly to temperature, and partly to the receptivity on the part of the muscle. It is found that with companion muscles taken from one animal and subjected to the action of equal quantities of nitrite, at a uniform temperature an almost identical result will be obtained; but if the temperature is higher to which one muscle is exposed, this will determine a more rapid contraction in it, than in the other exposed at a lower temperature. The influence of temperature is not the only cause of variation, however, for when corresponding muscles of two different animals are exposed to equal quantities of nitrite at a uniform temperature, very different results may be obtained. It is evident that there exists a variation in the susceptibility or receptivity of muscles of different Frogs to the effect of the volatile nitrite. The size of muscle did not vary to any appreciable extent, as the Frogs employed in this series of experiments were selected of a nearly uniform weight, varying only from 33 grms. to 35 grms. per individual.

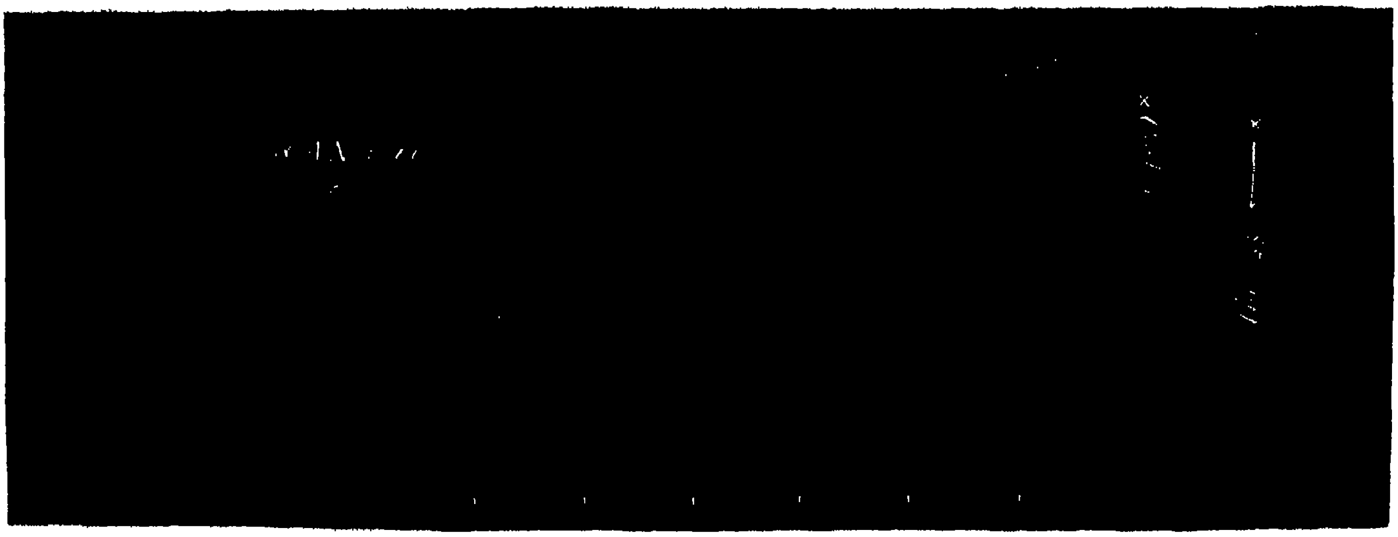
(*b.*) *On Stimulated Muscle.—Effect of α-amyl nitrite* on muscle contracting by periodic stimulation, one opening and one closing maximal shock being administered every 10 seconds weight 7·5 grms. (axial), lever unsupported.

If stimulation has been steadily carried on before the nitrite is admitted, so that the summit of the opening contractions and the basal junction lines are parallel, it will be found that after admission of nitrite, the stimulation being continued, the two lines, if not approximating, continue parallel. No increase of contractile power is observed except that occurring as a result of periodic stimulation of the muscle under an extending weight, nor in cases in which sub-maximal stimulation is used does the contraction become more extensive. Neither is the minimal irritability, as measured by distancing and approximating the secondary from the primary coil, increased by amyl nitrite. After the contractions have remained of equal value for a few minutes after admission of nitrite, or have even diminished a few millims. in extent, the basal line begins to rise, and the value of each contraction to decline slightly. This condition is not maintained steadily till contraction ceases. The basal line usually shows a more or less abrupt rise succeeded by a notch indicative of a partial pause, which strongly reminds one of the notch as seen in the veratria muscle contraction registered upon a rapidly moving surface; this is succeeded by a further rise, and occasionally by a second notch, passing on to the establishment of an irreducible rigor, and the entire cessation of active contraction. This notch is occasionally seen in an unstimulated muscle exposed to nitrite vapour. The experiment from which fig. 30 is taken, may serve to illustrate these points:—

Non-curarized gastrocnemius of *Rana temporaria* axial weight 7·5 grms. One opening and one closing shock in 10 seconds, temperature 14°·5 C., lever × 11, admit $\frac{1}{60}$ cub. centim. pure α-amyl nitrite (= 0·0146 grm.; NO_2 = 0·00576 grm.). Tracing 30.

1 minute active opening contraction	17 millims.	Slight shortening of muscle commencing.
2 minutes opening contraction.	17 ,,	Shortening of 1 minute.
4 ,, ,, ,,	14·5 ,,	9 millims. (first notch.)
6 ,, ,, ,,	11·5 ,,	14·5 ,,
8 ,, ,, ,,	6·5 ,,	2 ,,
10 ,, ,, ,,	4 ,,	27·5 ,, (second notch.)
12 ,, ,, ,,	1·5 ,,	30·5 ,,
14 ,, ,, ,,	ceased	33 ,,
16 ,, ,, ,,	,,	35 ,,

Tracing 30.



Action of α-amyl nitrite on actively contracting muscle. (See protocol.)

The closing stimulation ceases to be steadily operative before distinct shortening of the muscle appears. At a certain stage the action of the nitrite may be suspended, unless a large dose has been employed, and the muscle is rapidly passing into rigor, by emptying the chamber, either by washing out with fresh air or salt solution. It is only, however, during the earliest stages of shortening of a muscle, that a partial restitution of its length and power follows such a proceeding; under a more advanced action of the nitrite, the shortening and the impairment of the active contractions continue. Very small doses of amyl nitrite ($\frac{1}{100}$ cub. centim. = 0·0022 grm.; NO_2 = 0·000865 grm.) tend to weaken and ultimately to abolish active contraction in response to stimulation, without markedly raising the basal line.

Having now recorded the action of pure α-amyl nitrite on striated muscle, the consideration of other amyl compounds containing a known quantity of β-nitrite in addition to the α-nitrite will be made.

In addition to pure amyl nitrite the following were examined :—

Amyl nitrite consisting of	α-nitrite	88·6 per cent.	Marked II.
	β- „	11·4 „ „	
„ „ „	α- „	84·6 „ „	„ III.
	β- „	15·4 „ „	
„ „ „	α- „	95 „ „	„ I.
	β- „	5	

If we contrast the action upon muscles of the first of these (II.) in which a large proportion of β-amyl nitrite occurs with the pure α-amyl nitrite, it is seen that the latter causes a more rapid shortening, and an earlier and more pronounced rigor than the former. The pure α-amyl nitrite causes a more abrupt decline of active contractions when stimulation is made. The mixed nitrite (I.) containing a relatively larger proportion of pure α-amyl nitrite than (II.), was distinctly stronger than (II.), approaching near to the pure α-amyl nitrite in its action.

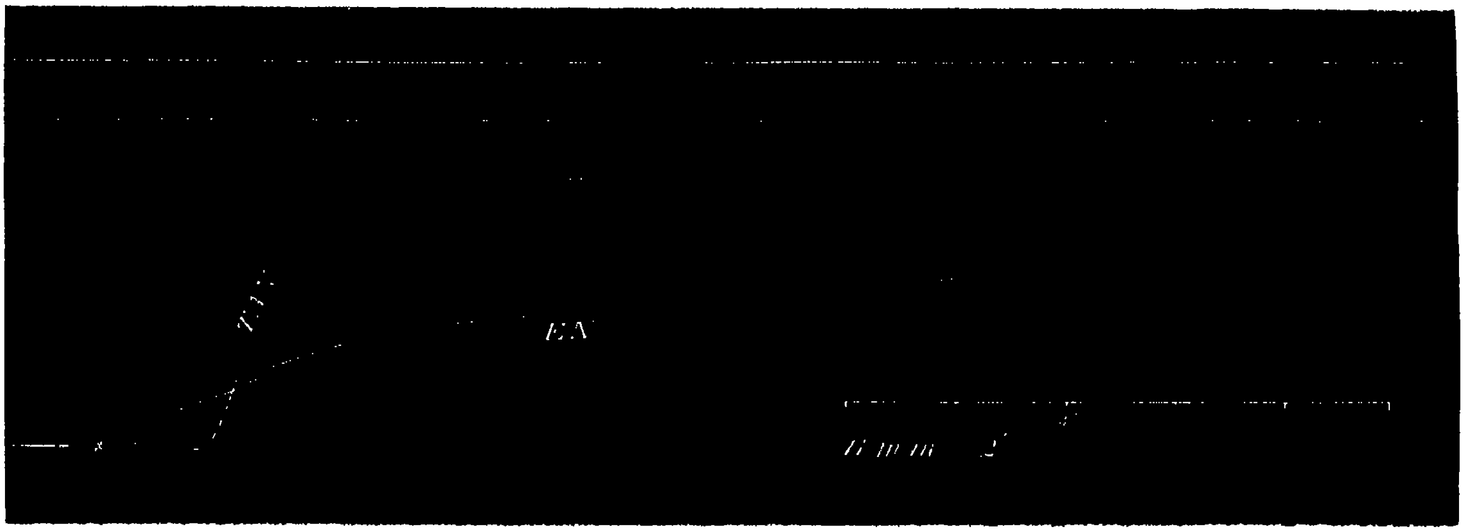
So far the series is regular, the effect declining with the introduction of β-nitrite; but on examining another nitrite (III.), containing even more (15·4 per cent.) of β-nitrite, it was found that it is more active than (II.), approximating to, though feebler than (I.), in its effect.

We are not justified, therefore, by taking the series as it stands, in recognising the relative reduction in the proportion of α-nitrite, or the relative increase in the proportion of β-nitrite as the sole cause of diminished action. Up to a certain point the series appears to follow this rule, but the body which, from the fact of its containing the largest amount of β-nitrite, might be expected to prove weakest, turns out stronger in its effect than the body containing somewhat less of β-nitrite. An examination of the relative degree of contraction produced by α-amyl and other bodies of the nitrite series shows the former to be inferior to all the butyl (tracing 33) and propyl compounds, but stronger than ethyl (tracing 46) and methyl nitrites, whilst it is to be regarded as weaker than tertiary, but stronger than secondary amyl nitrite. It is also low in the series when rapidity of production of primary effect is considered. In this respect it is equal with β-amyl nitrite, more active than normal and iso-butyl nitrite, but inferior to the rest of the group.

Tertiary Amyl Nitrite.

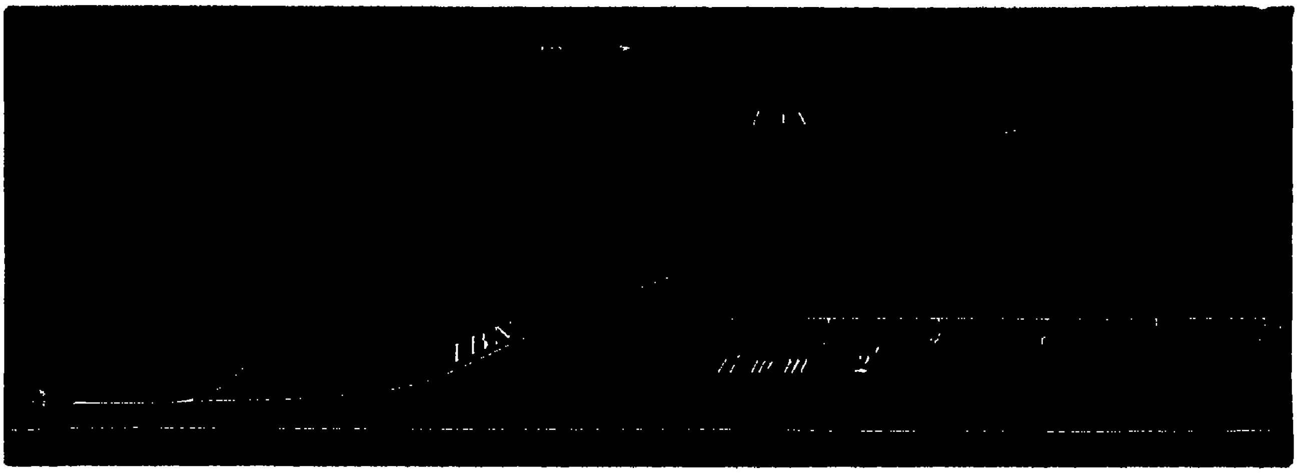
The muscular shortening produced by tertiary amyl nitrite is peculiar on account of its relatively rapid appearance and of the speed with which it passes to an approximate maximum. The rise of the lever occasioned is abrupt and extensive. Three bodies of the series of nitrites examined appear to cause an earlier contraction (the amount by volume and the temperature being equal), these are the ethyl (tracing 32), and methyl, and the secondary propyl compounds. (See tracings 45*a* and *b*, also tracing 43.) As the contraction, when it commences after tertiary amyl, proceeds very rapidly, the extent of the shortening at an early stage is greater than that of iso-butyl nitrite, which, though invariably stronger 30 minutes after application is slower in its first development. The total muscular shortening occasioned by the former, is, however, only distinctly exceeded by the latter, it is very slightly stronger than secondary propyl nitrite (see tracings 43 and 45, *a* and *b*), and the other members of the series succeed it.

Tracing 31.



Contrasted action of tertiary amyl and ethyl nitrites on resting muscle. (See protocol.)

Tracing 32.



Contrasted action of tertiary amyl and iso-butyl nitrites on resting muscle. (See protocol.)

In the following table it is contrasted with Iso-butyl Nitrite, Ethyl Nitrite, and Secondary Propyl Nitrite respectively :—

Date.	Nitrite.	Dose.	Weight.	Temperature.	Lever.	Time of first contraction after introduction into muscle chamber.	Extent of shortening of muscle in—						
							5 mins.	10 mins.	15 mins.	18 mins.	25 mins.	30 mins.	60 mins.
			grm.	° C.		secs.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
27.3.90 tracing 31	Tertiary amyl . .	$\frac{1}{100}$ cub. centim. (= ·0089 grm.; NO_2 = ·0035 grm.)	10	10	× 11	138	11·5	25	..	27	27·5		
	Iso-butyl	$\frac{1}{100}$ cub. centim. (= ·0087 grm.; NO_2 = ·0038 grm.)	10	10	× 11	230	·5	·8	..	28	34		
25.3.90 tracing 32	Tertiary amyl . .	$\frac{1}{100}$ cub. centim. (= ·0089 grm.; NO_2 = ·0035 grm.)	10	10·25	× 11	106	22·5	27·5	28				
	Ethyl	$\frac{1}{100}$ cub. centim. (= ·0089 grm.; NO_2 = ·00545 grm.)	10	10·25	× 11	42	11·5	14	17				
25.11.90 tracings 45*a* and 45*b*	Tertiary amyl . .	$\frac{1}{200}$ cub. centim. (= ·00445 grm.; NO_2 = ·0035 grm.)	20	12·5	× 9	116	25	34	36·5	37	37·25	37·25	46
	Secondary propyl .	$\frac{1}{200}$ cub. centim. (= ·00435 grm.; NO_2 = ·00224 grm.)	20	12·5	× 9	78	8	20·5	24·25	32	33	34·25	40

The Butyl Compounds.

Of these the following have been examined :—

1. Primary butyl nitrite.
2. Iso-butyl nitrite.
3. Secondary butyl nitrite.
4. Tertiary butyl nitrite.

The action of members of this group, with one exception, is distinguished by its strength. Passive contraction of the muscle, followed by a well-marked rigor, occurs when a very dilute atmosphere of the nitrite is admitted to the muscle. Even so small an addition as the $\frac{1}{300}$ cub. centim. of some of these bodies may cause a distinct rigor.

This fact will of course suggest an early modification in active contraction resulting from stimulation. Active contraction is in fact rapidly abolished when the dose of nitrite is sufficient to develop rigor, and more slowly when the dose is too small to induce this condition.

In order of activity as regards strength of action on muscle, they take the following order :—

(1.) Iso-butyl nitrite.
(2.) Secondary butyl nitrite.
(3.) Tertiary butyl nitrite.
(4.) Normal butyl nitrite.

In speed of action they are placed thus :—

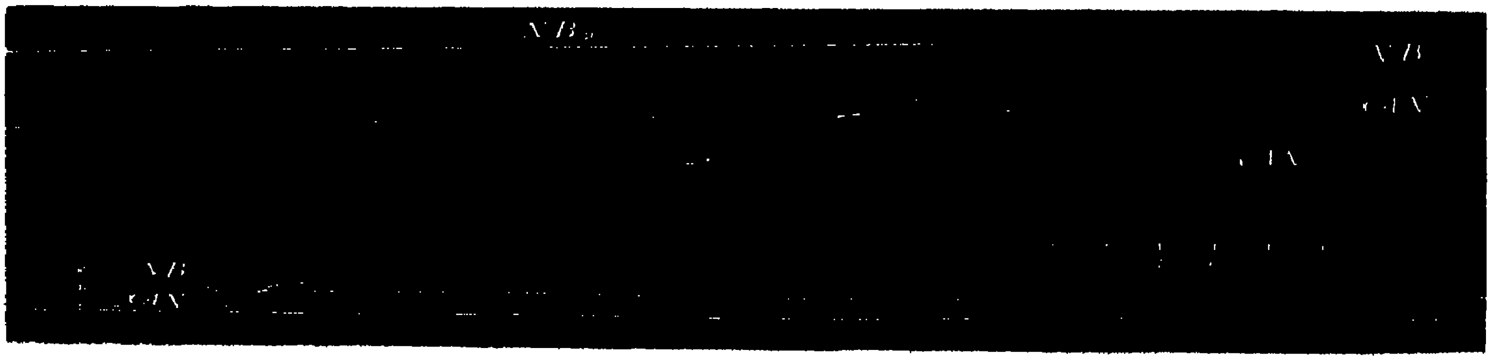
(1.) Tertiary butyl nitrite.
(2.) Secondary butyl nitrite.
(3 and 4.) Butyl and iso-butyl nitrites.

In the latter respect, though the tertiary is slightly earlier in its action than the secondary, the difference is by no means marked. The butyl and iso-butyl nitrites are so similar that it would not be warrantable to separate them.

Normal Butyl Nitrite.—This substance is the weakest of the butyl series as regards the extent of shortening it produces, and it even stands low in this respect in the general series. Thus it is to be placed after both iso-propyl and normal propyl, and secondary and tertiary butyl nitrite, although it is stronger than α-amyl nitrite and than ethyl and methyl nitrites.

In speed of action it is one of the latest; α-amyl nitrite produces shortening before it, whilst ethyl and methyl nitrites, the propyl and the other butyl compounds, with the exception of iso-butyl nitrite, which is about equal, are all more active.

Tracing 33.



Contracted action of butyl and α-amyl nitrites on resting muscle. (See protocol.)

When the rise of the basal line commences it is comparatively slow in reaching its maximum.

($\frac{1}{100}$ cub. centim. = 0·0088 grm.; NO_2 = 0·00393 grm.)

The following experiments will illustrate the relative effect of this nitrite compared with that of α-Amyl Nitrite and Secondary Propyl Nitrite respectively.

Date.	Nitrite.	Dose.	Temperature.	Weight. (lever.)	Length. (lever.)	Time of first contraction after introduction into muscle chamber.	Extent of shortening of muscle in—						
							5 mins.	10 mins.	15 mins.	20 mins.	25 mins.	30 mins.	60 mins.
			° C.	grms.		secs.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
13.11.90 tracing 33	Butyl	$\frac{1}{100}$ cub. centim. (= ·0088 grm. ; NO_2 = ·000393 grm.)	11	20	× 9	327	. .	3	10·5	21	29·5	37	46·5
	α-Amyl	$\frac{1}{100}$ cub. centim. . . .	11	20	× 9	218	1	11	21	28	31	33	35
13.11.90	Butyl	$\frac{1}{200}$ cub. centim. (= ·0044 grm. ; NO_2 = ·001965 grm.)	11·5	20	× 9	345	. .	2	4·5	6	6·25	7	10·5
	Secondary propyl .	$\frac{1}{200}$ cub. centim. (= ·00435 grm. ; NO_2 = ·0019 grm.)	11·5	20	× 9	180	1	3	5·5	7·5	10·5	12	15·5

Iso-butyl Nitrite.—This nitrite is interesting as being the most active substance in the series when judged by the extent of shortening which is produced, 30 minutes to 60 minutes, or at any subsequent time after its introduction into the muscle chamber; whilst it is almost at the other end of the series when the speed of the initial shortening is measured. In the former respect it is approached most nearly by tertiary amyl nitrite and secondary butyl nitrite; whilst in the latter it stands with normal butyl nitrite slightly below α-amyl nitrite.

Even such a small dose as the $\frac{1}{350}$ cub. centim. ($=$ 0·00248 grm.; $NO_2 =$ 0·001 grm.) is capable of causing a decided effect, as the following figures will demonstrate:—

Iso-butyl nitrite, $\frac{1}{350}$ cub. centim., introduced into the air-tight muscle-chamber, in which a gastrocnemius is contracting in response to maximal stimulation—(one opening and one closing stimulation every 10 seconds).

LEVER × 7. Weight 7·5 grms. (axial). Temperature 9°·5 C.

Time.	Maximal contraction (opening).	Elevation from abscissæ.
mins.	millims.	millims.
0	12	0
4	12	0
8	12	0
10	11·5	·75
14	11	2·5
18	9·5	5
22	7	10
26	5·5	11
30	2	12
34	0	13

Tracing 34.

Action of iso-butyl nitrite on contracting muscle.

The effect of a large dose upon an actively contracting muscle is well demonstrated by the following notes (tracing 34):—

Iso-butyl nitrite, $\frac{1}{60}$ cub. centim. (= 0·0145 grm.; NO_2 = 0·00633 grm.). Temperature 14° C. Gastrocnemius (non-curarized) in muscle-chamber.

LEVER × 11. Weight 7·5 grm. (axial). Stimulation as before.

Time.	Maximal contraction.	Elevation from abscissæ.
mins.	millims.	millims.
0	16·5	0
2	16·5	1·25
4	11	13
6	5	23
8	4·5	32
10	2	37
12	·5	40·5
14	0	42
16	0	43
18	0	43·5
20	0	44

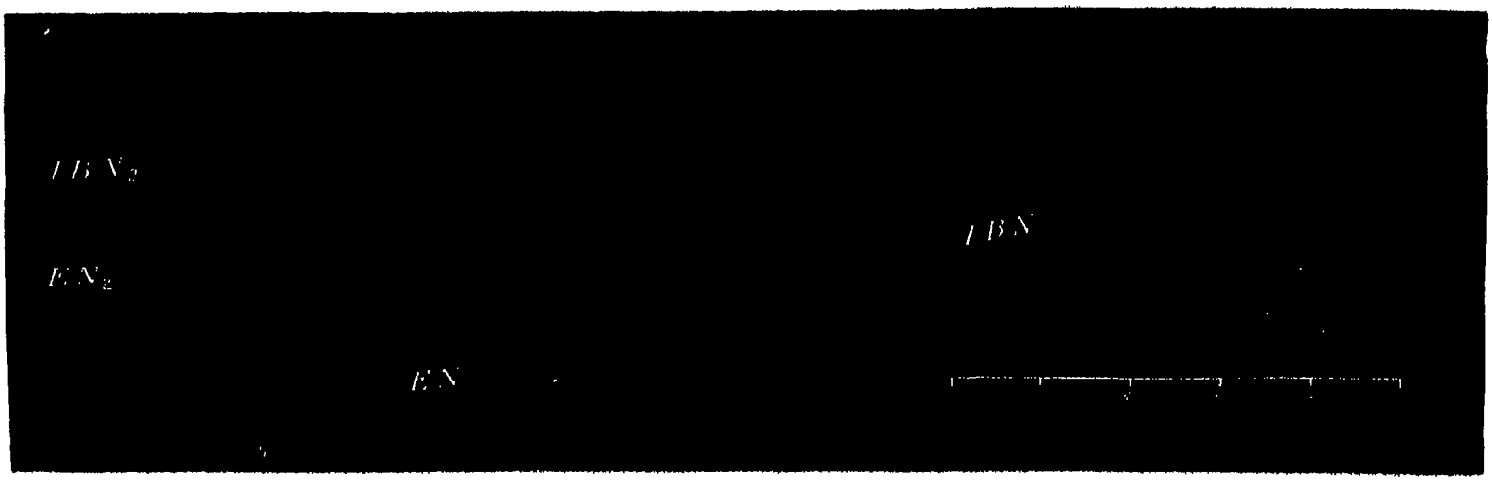
The muscle was in white rigor. This tracing may be contrasted with tracing 30 in which α-amyl nitrite was applied to the companion muscle under exactly similar conditions.

It will thus be seen that in an air-tight chamber whilst extremely small quantities of iso-butyl nitrite vapour produce a marked effect upon active and passive contraction of striated muscle, in larger amounts the effect becomes a very powerful one.

The basal curve of active contraction is peculiar, as many of those caused by the nitrites are, in showing when the record is made upon a slowly moving surface, two notches in its ascent, which bring to mind the summation of stimulations in a muscle exposed to induction shocks delivered rapidly, and even more to the peculiar summated appearance observable at the commencement of contraction of the veratrine muscle, when its contraction is recorded on a rapidly moving surface.

A contrasted experiment between iso-butyl nitrite and ethyl nitrites, in which no stimulation was made, may be shortly mentioned here. (Tracing 35.)

Tracing 35.



Contrasted action of iso-butyl and ethyl nitrites upon resting muscle. (See protocol.)

Amount.	Weight.	Temperature.	Lever.	Time of first contraction after introduction into muscle-chamber.	Extent of shortening of muscle in		
					5 mins.	10 mins.	20 mins.
	grms.	°F.		secs.	mm.	mm.	mm.
17.3.90.							
Iso-butyl nitrite, $\frac{1}{100}$ cub. centim. (= 0·0087 grm.; NO_2 = 0·0038 grm.)	7·5	54	×6	196	2·5	14·5	25
Ethyl nitrite, $\frac{1}{100}$ cub. centim. (= 0·0089 grm.; NO_2 = 0·00545 grm.)	7·5	54	×6	76	6	9·5	14

Although in this experiment the reaction of the muscle is not vigorous, the relationship between the two nitrites as to speed and extent of contraction occasioned is preserved. (See also tracings 36, 38, 44, and 48.)

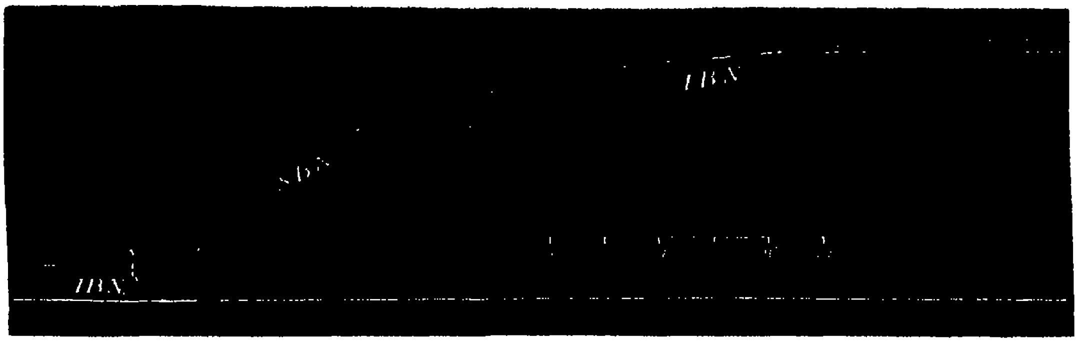
Secondary Butyl Nitrite.—In strength of effect this compound comes after iso-butyl and tertiary amyl nitrites; it is near to secondary propyl nitrite, than which it is slightly stronger. It does not cause the abrupt rise of the lever which the tertiary compound produces.

In speed of action it appears to be after the propyl nitrites, and slightly after tertiary butyl nitrite; it is therefore a long way behind the methyl and ethyl compounds in this respect.

The α-amyl nitrite and both iso-butyl and normal butyl nitrites are slower in their action.

The following experiment will serve to contrast the effect of iso-butyl and secondary butyl nitrites upon the resting muscle.

Tracing 36.



Contrasted action of secondary butyl and iso-butyl nitrites on resting muscle. (See protocol.)

Companion gastrocnemii of frog of 27 grms. Weighted with 7·5 grm. (axial.) Lever × 11. Temperature, 11°·5 C. (Tracing 36.)

To No. 1 admit $\frac{1}{200}$ cub. centim. iso-butyl nitrite.
„ 2 „ „ secondary „

Time.	Shortening.	
	1	2
secs.		
82	..	commenced
120	commenced	
240	4 millims.	13 millims.
480	17·5 „	26 „
960	36·5 „	37 „
1440	45 „	42 „
1920	47·5 „	42·5 „

The activity of secondary butyl nitrite with reference to muscle runs very parallel with that of the secondary propyl compound (see tracing 37, *a* and *b*). The latter, however, whilst occasioning a somewhat more rapid occurrence of passive contraction does not produce the same degree of shortening of the muscle after 30 minutes' application, nor does it so rapidly abolish active contraction, if this is in progress from stimulation. If, during the early elevation of the basal line from the effect of secondary butyl or other nitrites, the muscle which has been stimulated periodically is allowed to rest for a short time, it will be observed that relaxation takes place, the lever sinking to a position distinctly below that of the basal line at the time the active contraction ceased. The first active contraction when stimulation is resumed is an extensive one, but thereafter the basal line rises in sequence to its former course. This result can be obtained steadily, though in progressively diminishing extent, so long as the muscle contracts actively, but after it has ceased to respond to stimulation relaxation is no longer witnessed, excepting some hours later, when, if a heavy weight and a comparatively small amount of nitrite has been employed, some relaxation may occasionally be witnessed. In the early stages of its action the shortening of the muscle is in excess of the rigor produced, and the difference between the two is attributable to a retardation in relaxation after active contraction, which occasions a temporary shortening, when stimulation recurs with sufficient rapidity. The following experiment, whilst serving to contrast the secondary butyl and propyl nitrites, will also show the result of a pause in the course of stimulation.

The two gastrocnemii of a frog of 26 grms. are exposed in succession to the $\frac{1}{200}$ cub. centim. of secondary butyl (1) and secondary propyl nitrites (2) respectively, after maximal stimulation (one opening shock every 4 seconds, the closing shock being cut out) had been admitted for 3 minutes (tracing 37, *a* and *b*).

Weight 20 grms. (axial). Lever × 9. Temperature 8°·5 C. Tracing 37, *a* and *b*.

	Time.	(1.)		(2.)	
		Active contraction.	Basal line shortening.	Active contraction.	Basal line shortening.
	secs.	millims.	millims.	millims.	millims.
	..	22	0	23·5	0
Introduce nitrites . .	0				
	32	..	..	24	commences
	50	22·5	commences		
	240	20·5	10·5	20·5	12·5
	480	7·5	26	14	26
	720	4·5	30·5	8·5	29
	960	·5	31	2·5	27·5
	1070	ceased			
	1200	..	..	ceased	27

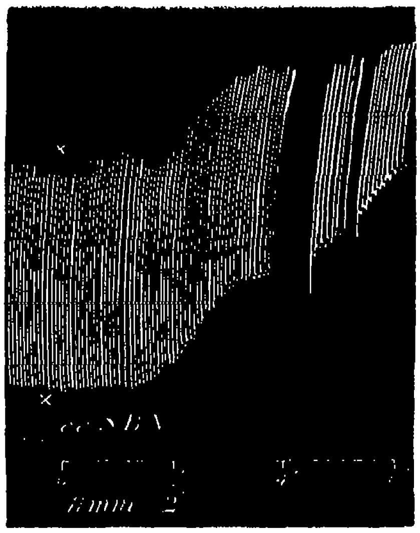
Secondary propyl nitrite shows a somewhat earlier shortening, a less extensive rigor, and a later abolition of active contraction. The difference between these two nitrites is, however, never an extensive one.

Tertiary Butyl Nitrite.—The curve of passive contraction of the tertiary butyl compound is peculiar and distinctive, the action of the drug producing a passive contraction of muscle which proceeds with great rapidity. In one experiment, $\frac{1}{100}$ cub. centim. was introduced into a chamber containing a resting muscle. Shortening commenced in 2 minutes 30 seconds, and the muscle passed with great rapidity into further contraction and rigor, so that in 5 minutes a degree of contraction was reached which did not markedly increase for over 30 minutes afterwards. The total shortening effect is small when compared with that of iso-butyl nitrite, but it is sooner developed, the maximum being relatively much more rapidly attained.

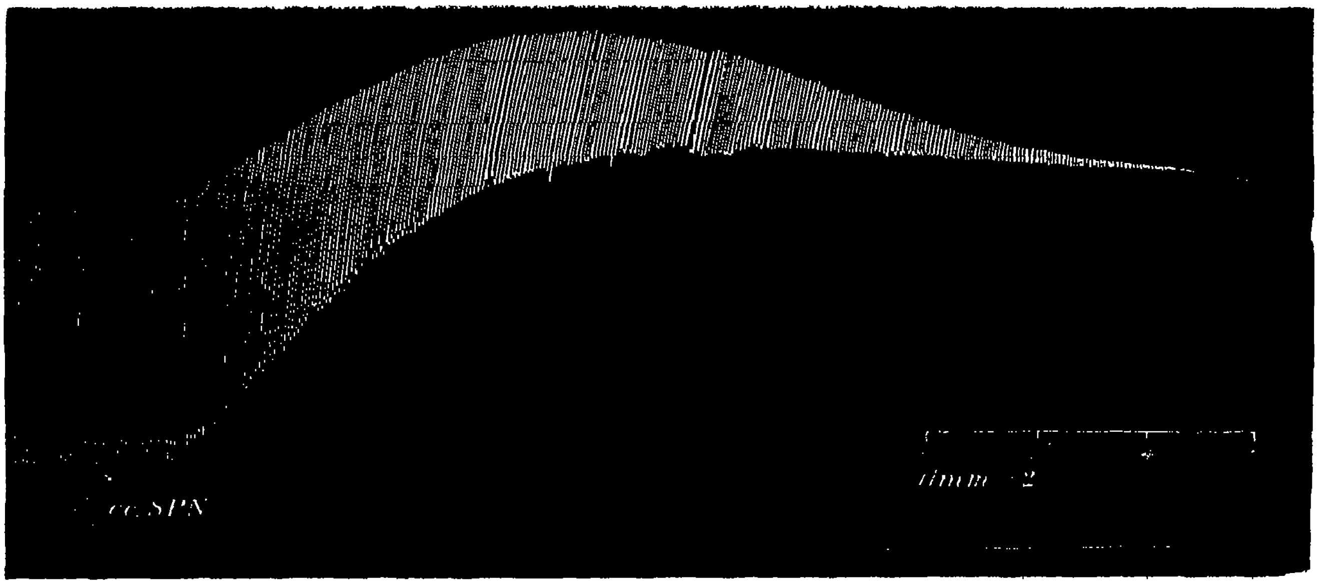
The contraction produced by iso-butyl nitrite is relatively slower in appearing, the ascent of the curve is more gradual, but it is continuous until a distinctly higher level is reached than in the case of the tertiary compound. Response to stimulation ceases sooner in the case of the former.

The following experiments serve to contrast the effects of iso-butyl nitrite and tertiary butyl nitrite. The extent of the action of the former in contrast with the latter is somewhat excessive, but the contraction is highly characteristic in each instance.

Tracing 37*a*.



Tracing 37*b*.



Contrasted action of secondary butyl and secondary propyl nitrites upon actively contracting muscle. Stimulation is twice interrupted in the case of the former. (See protocol.)

Experiment.—Contrasted action of two companion muscles placed successively in an air-tight chamber (gastrocnemius of *Rana temporaria*) 10°·5 C. Weight 7·5 grms. (axial). Lever × 7. No stimulation. (Tracing 38.)

Tracing 38.

Contrasted action of tertiary butyl and iso-butyl nitrites upon resting muscle. (See protocol.)

	Time.	Passive contraction.		Passive contraction.
	secs.	millims.		millims.
Admit $\frac{1}{200}$ cub. centim. (= 0·0435 grm.; NO_2 = 0·0019 grm.) iso-butyl nitrite	0	..	Admit $\frac{1}{200}$ cub. centim. (= 0·0043 grm.; NO_2 = 0·00189 grm.) tertiary butyl nitrite	
	229			begins
	316	begins		
	420	5		15·5
	660	24·5		21·5
				(curves cross here)
	900	32		22
	1140	39		22
	1380	41		22·5
	1620	42·5		22·5
	1860	43·5		22·5

Both the muscles, but especially that exposed to iso-butyl nitrite, were in a state of opaque white rigor.

(25.7.90.) Tertiary butyl nitrite, when admitted to an air-tight muscle-chamber in which a muscle is periodically contracting, causes the basal line to rise rapidly, and soon abolishes response to stimulation. Gastrocnemius of frog in air-tight chamber one opening and one closing maximal stimulation every 10 seconds. Lever × 7. Weight 10 grms. (axial). Temperature 15°·3 C. Opening contraction 14·5 millims. (Tracing 39.)

	Time.	Passive shortening.	Active contraction.
	secs.	millims.	millims.
Admit $\frac{1}{100}$ cub. centim. (= 0·0086 grm.; NO_2 = 0·00378 grm.). Tertiary butyl nitrite	0		
	109	Shortening commences	13·5
	120	2	13·5
	240	22	3·5
	480	28	1
	720	28·5	Ceased
	960	28·5	
	2160	28·75 Muscle in white rigor	

The position of tertiary butyl nitrite in the series, as regards the shortening of muscular tissue it ultimately produces, appears to be above normal butyl nitrite, whilst [illegible] to both the other butyl compounds, to tertiary amyl and to secondary propyl nitrite. With reference to the length of time elapsing between the introduction of nitrite and the first evidence of passive contraction, it stands below the propyl compounds and above normal butyl nitrite. The rapid development of passive muscular contraction it occasions is most closely approached by tertiary amyl nitrite.

Tracing 39.

Action of tertiary butyl nitrite on actively contracting muscle. (See protocol.)

Contrasting the butyl series with the amyl nitrites it may be stated, in general terms, that the former are distinctly more vigorous in their action, in so far as the shortening produced in striated muscular tissue is considered; an exception must, however, be made in the case of tertiary amyl nitrite, which exceeds all the butyl compounds in this respect, excepting the iso-butyl nitrite. Butyl and iso-butyl nitrites give rise to a shortening which has its first appearance after that produced by α-amyl and α- with β-amyl nitrites. The secondary and tertiary butyl nitrites are more rapid, but less so than tertiary amyl nitrite.

The Propyl Nitrites.

The primary propyl and secondary propyl compounds were examined. Of these two bodies, propyl nitrite is the weaker in its total effect upon muscle shortening. It is, however, rapid in action, so that in this respect it stands, with the exception of tertiary amyl and secondary propyl nitrite, the ethyl and methyl compounds, at the head of the list.

Contrasted with the other nitrites enumerated below, the same volume of each of these and of propyl nitrite being employed in each experiment, the results are as follows :—

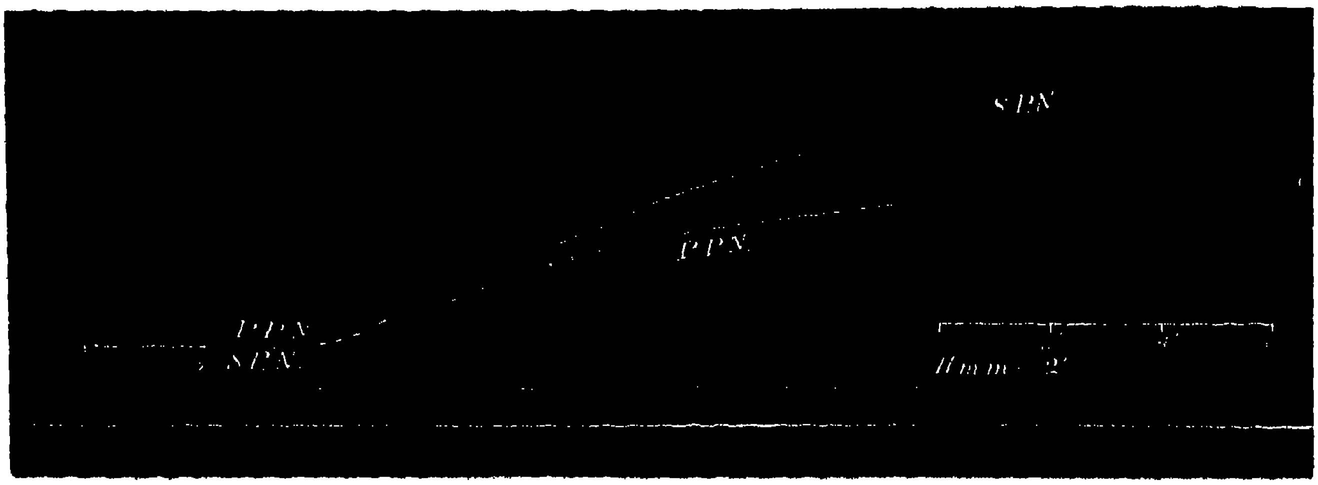
Ethyl nitrite causes an earlier contraction, but propyl nitrite a greater shortening.

Tracing 40.

Action of primary propyl nitrite on resting muscle. The curve of ethyl nitrite is not given. (See protocol.)

Secondary propyl nitrite acts very slightly sooner, and is distinctly stronger than the primary compound.

Tracing 41.



Contrasted action of primary and secondary propyl nitrites on resting muscle. (See protocol.)

α-Amyl nitrite causes a later contraction and a weaker shortening effect.

Tertiary amyl nitrite is slightly more rapid in causing shortening, and produces more powerful shortening.

A few figures will give a general indication of the difference of reaction. All are taken from the gastrocnemius excepting the last, which is from the triceps.

Nitrite.	Dose.	Temperature.	Weight.	Lever.	Initial shortening.	Passive shortening in—		
						15 mins.	30 mins.	60 mins.
	cub. centim.	° C.	grm.		secs.	mm.	mm.	mm.
Propyl* . . . . Ethyl . . . . (tracing 40)	$\frac{1}{100}$	7·75	10	× 9	240 130	10 13	19·5 19	Much stronger.
Primary propyl . Secondary propyl (tracing 41)	$\frac{1}{200}$	12·5	20	× 9	82 77	22 14·5	.. ..	27 38
Propyl . . . . α-Amyl	$\frac{1}{200}$	14·5	10	× 9	109 185	22·5 15·5	23 17	31·5 24
Propyl . . . . Tertiary amyl .	$\frac{1}{300}$	12·6	10	× 11	240 189	24 34	34 37	

The action of primary propyl nitrite upon a contracting muscle is well illustrated by the following experiment. (Tracing 42.)

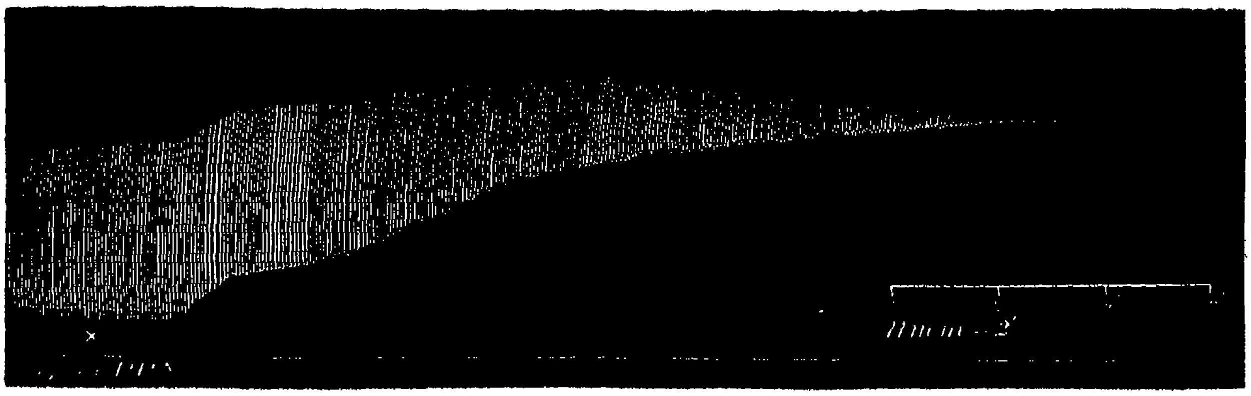
An opening stimulation was delivered to the gastrocnemius every 4 seconds. Temperature, 16° C. Weight, 7·5 grms. (axial). Lever × 7.

---

* Both the muscles in this experiment yielded a passive shortening with a notch. This is interesting, as though seldom witnessed in absence of stimulation, it is very frequent during its occurrence.

	Time.	Passive shortening.	Active contraction.
	secs.	millims.	millims.
Admit $\frac{1}{250}$ cub. centim. primary propyl nitrite. (= 0·0018 grm.; NO_2 = 0·00061 grm.).	0	..	16·5
	98	Commences	16·5
	240	4	16
	480	12·5	11
	720	16	5·5
	960	18	1·75
	1200	19	Ceased.

Tracing 42.



Action of primary propyl nitrite on actively contracting muscle. (See protocol.)

Two distinct periods of arrest of passive shortening of the muscle will be observed in this curve, one being within 1 minute of commencing contraction, the second 3 minutes later.

Tracing 43.

Contrasted action of secondary propyl and tertiary amyl nitrites on resting muscle. (See protocol.)

Secondary Propyl Nitrite.—This is a more active body than propyl nitrite, it is not far behind secondary butyl nitrite (tracing 37*a*) and tertiary amyl nitrite in the extent of the contraction it occasions. It produces its initial effect also with rapidity, though it is much behind methyl and ethyl nitrites. In this respect it stands near to tertiary amyl and primary propyl nitrite. The passive muscular contraction does not pass on to an approximate maximum nearly so rapidly as after the exposure of a muscle to an equal dose of tertiary amyl or tertiary butyl nitrite.

The following figures will serve to show the relative difference in reaction of muscles to iso-butyl and other nitrites.

Tracing 44.

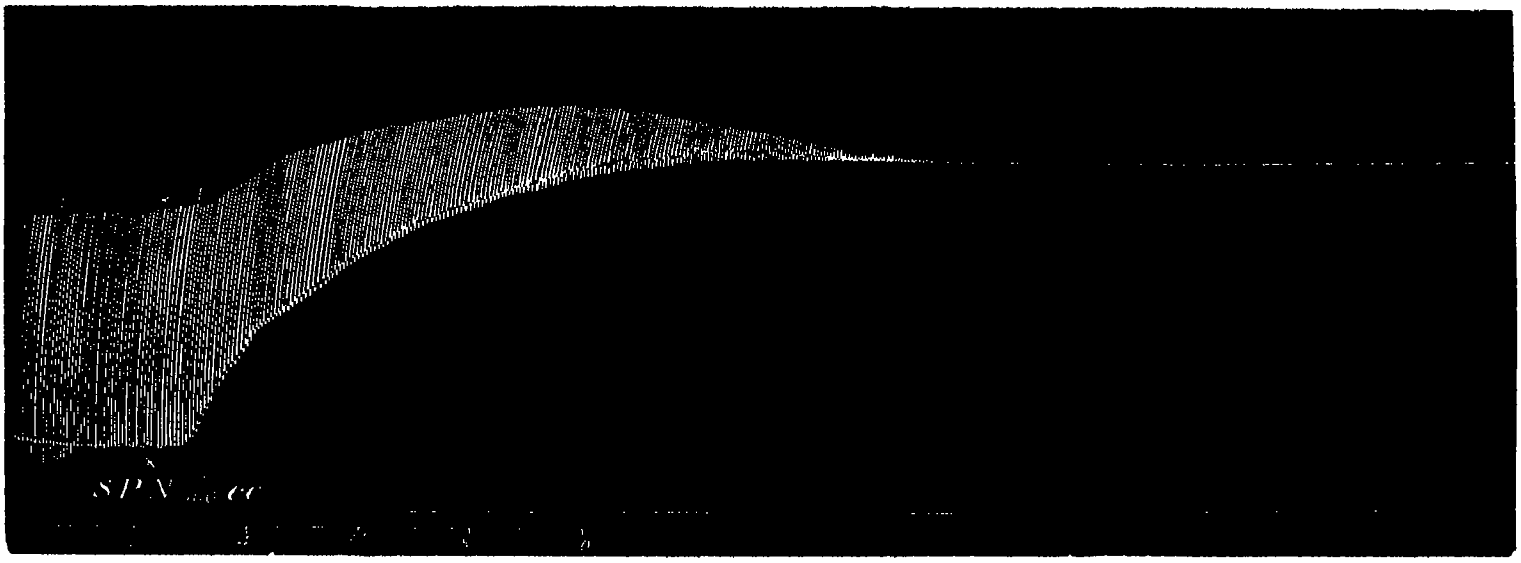
Contrasted action of secondary propyl and iso-butyl nitrites on resting muscle. (See protocol.)

Nitrite.	Dose.	Temperature.	Weight.	Lever.	Initial shortening.	Passive shortening in— 15 mins.	30 mins.	45 mins.	60 mins.
	cub. centim.	° C.	grms.		secs.	mm.	mm.	mm.	mm.
Secondary propyl	$\frac{1}{100}$	12	2·20	× 9	65	22·5	24·5		
Secondary butyl					95	24·5	27·5		
Secondary propyl	$\frac{1}{100}$	9·5	20	× 9	92	32	38		
Tertiary amyl (tracing 43)					109	39·5	43·5		
Secondary propyl	[illegible]	11·5	20	× 9	114	24	32		
Iso-butyl (tracing 44)					202	25	26		

On [illegible] secondary propyl nitrite is powerfully active. It abolishes active contraction rapidly though less so than equal volume of secondary butyl nitrite, which is therefore to be classified as slightly stronger. The experiment (tracing 37*a*) must be referred to and contrasted with tracing 37*b* secondary propyl nitrite taken from the companion muscle. The passive shortening of the latter is rather less whilst the abolition of active contraction is relatively later. These points are still more clear when tertiary amyl and iso-butyl are contrasted with the secondary propyl nitrites. We shall only introduce one example of an experiment in which this contrast was made.

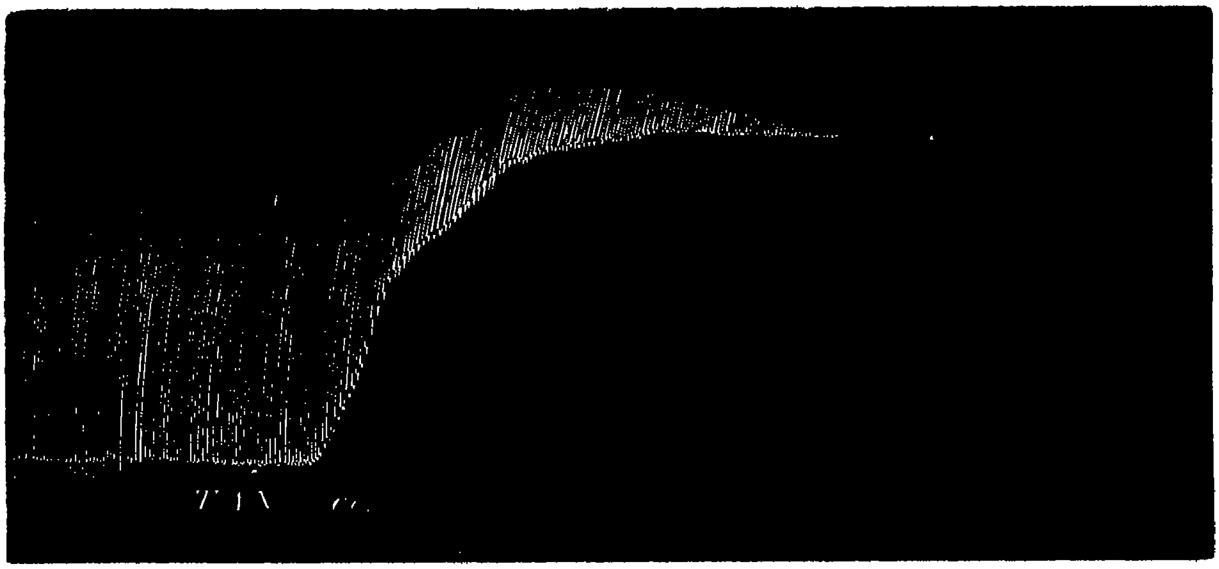
(12.2.90. Tracing 45, *a* and *b*.) Gastrocnemii of small frog of 20 grms. Stimulation by one (opening) induction shock every 4 seconds. To one muscle, $\frac{1}{100}$ cub. centim. tertiary amyl nitrite (tracing 45*a*) was conveyed in the air-tight chamber, to the other $\frac{1}{100}$ cub. centim. secondary propyl nitrite (tracing 45*b*). Weight, 20 grms. Lever × 9. Temperature, 8°·5 C.

Tracing 45*a*.



Action of secondary propyl nitrite upon actively contracting muscle. Contrast with tracing 45*b*. (See protocol.)

Tracing 45*b*.



Action of tertiary amyl nitrite upon actively contracting muscle. Contrast with tracing 45*a*. (See protocol.)

Time.	Secondary propyl nitrite.		Tertiary amyl nitrite.	
	Basal line elevation.	Active contraction in—	Basal line elevation.	Active contraction in—
secs.	millims.	millims.		millims.
0	0	24	0	26
50	Commenced	..	Commenced	
65				
120	10·5	16·5	9	18
240	19	13·5	24	8·5
480	26·5	8	32	3·5
660	..	..	..	Ceased
720	28	1·75	31	
880	..	Ceased		
960	27·5	..	31·5	
1200	27·5	..	31·5	
1440	28			

The result of this experiment is, in all respects, characteristic of the difference between the two nitrites examined. Tertiary amyl nitrite causes shortening slightly later, but this proceeds more rapidly when it is established, it also abolishes active contraction more speedily than secondary propyl nitrite does.

Ethyl Nitrite.—On account of its low boiling-point (17° C.), and the consequent danger of loss by evaporation, this substance has to be handled with great care. The temperature of the measuring pipette and bottle must be kept down by immersion in ice. By adopting such and other precautions, which a little experience in working with this substance showed to be necessary, the experiments were, it is believed, made free from error.

The initial passive contraction of a muscle exposed to vapour of ethyl nitrite is rapid in making its appearance, more so than all other members of the series examined, with the exception of methyl nitrite.

Extent of dose introduced, temperature under which the experiment is conducted, etc., produce modification in speed of action, as in the case of all other nitrites.

Unless the dose of ethyl nitrite administered is large, the total shortening of the muscle which such an amount is capable of causing is only gradually produced, and in this respect ethyl differs [illegible] tertiary amyl nitrites, which occasion a rapid shortening of the muscle approximating to the maximal effect realizable from such small doses. With large doses of ethyl nitrite an approximate maximum is rapidly produced. If stimulation is admitted, the individual contractions rapidly decline in extent as the basal line rises, and in a few minutes these are suspended altogether.

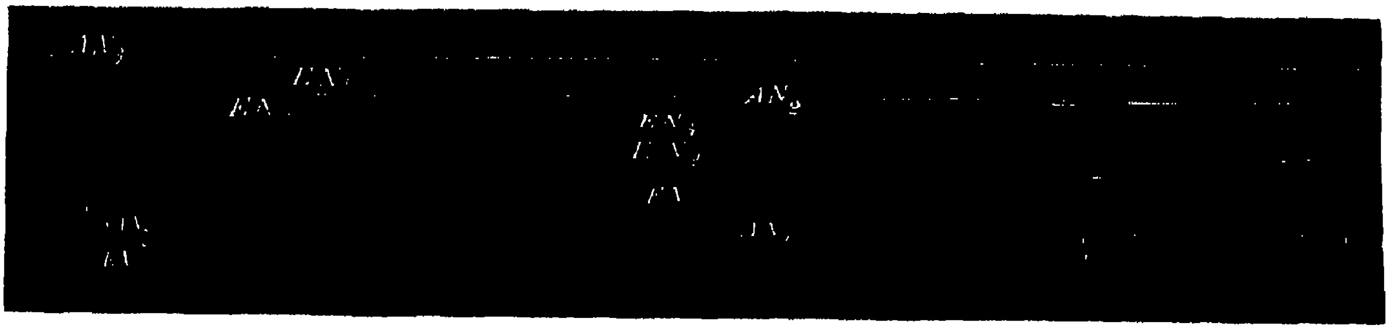
The following figures will indicate the course of an experiment:—

Two (companion) gastrocnemii were subjected to the action of amyl nitrite and ethyl nitrite respectively.

The original basal line of the two is coincident.

(14.3.90.) *Experiment.* 15 minutes drum; 32 millims. = 2 minutes.—Gastrocnemius of frog. Lever × 11. Weight 10 grms. (axial). Temperature 14° C. Tracing 46.

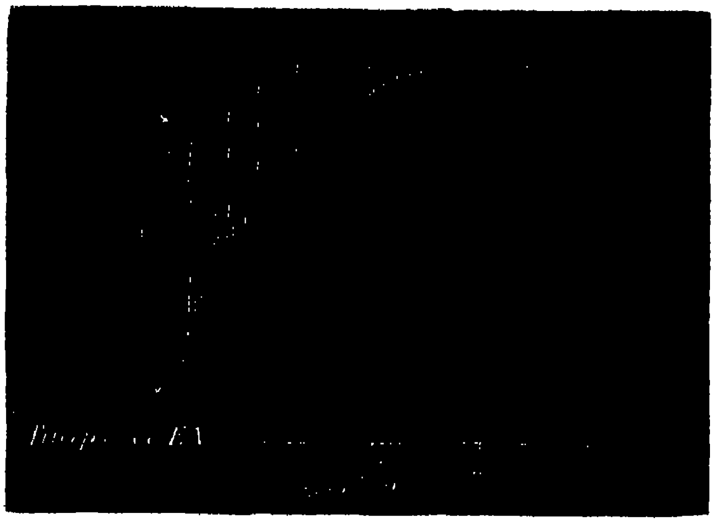
Tracing 46.



Contrasted action of ethyl and amyl nitrite on resting muscle. (See protocol.)

Time.	Ethyl Nitrite.	α-Amyl Nitrite.
secs.		
0	Admit $\frac{1}{50}$ cub. centim. (= 0·00178 grm.; NO_2 = 0·0109 grm.)	Admit $\frac{1}{50}$ cub. centim. (= 0·0176 grm.; NO_2 = 0·0076 grm. α-amyl nitrite)
41	Contraction commences	
120	6·5 millims.	
150	..	Contraction commences
240	9·5 ,,	2 millims.
480	10 ,,	12 ,,
900	12 ,,	21·5 ,,
1800	17·5 ,,	29 ,,

Tracing 47.



Action of ethyl nitrite on actively contracting muscle. (See protocol.)

(27.7.90.) *Experiment* in which stimulation is made, is taken from a triceps burdened with 10 grms. Axial weight. Lever × 7. Temperature 13°·3 C. Tracing 47.

	Time.	Active contraction on stimulation.	Passive shortening.
	secs.		
Admit $\frac{1}{10}$ cub. centim. (= 0·0127 grm.; NO_2 = 0·0079 grm.) ethyl nitrite to the muscle-chamber	0	22 millims.	
	42		Commences
	120	13	13 millims.
	240	3·5	23·5 "
	360	1	28 "
	495	Ceases	28·5 "

As exhibiting the speed of appearance of initial contraction and the extent of the effect produced, the following figures may serve as illustrations. The curve of ethyl nitrite was, however, taken at a lower temperature than that of iso-butyl nitrite. Tracing 48.

Tracing 48.

Contrasted action of ethyl and iso-butyl nitrite on resting muscle. (See protocol.)

Substance.	Dose.	Lever.	Weight.	Temperature.	Initial contraction.	Shortening.					
						5 mins.	10 mins.	20 mins.	40 mins.	80 mins.	160 mins.
			grm.	° C.	secs.	mm.	mm.	mm.	mm.	mm.	mm.
Ethyl nitrite	$\frac{1}{100}$ cub. centim. (= 0·0089 grm.; NO_2=0·00545 grm.)	×6	7·5	11·5	54	7·5	9·5	10·5	14		
Iso-butyl nitrite	$\frac{1}{100}$ cub. centim. (= 0·0087 grm.; NO_2=0·0038 grm.)	×6	7·5	12·5	98	17	26	31	39·5		

Tracings 31 and 35 also illustrate speed and manner of action of small doses. As regards extent of contraction occasioned, ethyl nitrite is inferior to all the other nitrites excepting methyl; it comes after amyl nitrite in this respect.

Methyl Nitrite.—As already stated, this body was prepared in the gaseous form for use in bulbs having a measured capacity. These bulbs were filled at a noted temperature and pressure.

Before the experiment commenced, the muscle cylinder was partly filled with salt solution. The bulb was brought into connection with a glass tube situated high up on the side of the cylinder, and to its lower end was attached a rubber tube connecting it with a syringe charged with salt solution. The ends of the bulb were broken within the tubes, and the salt solution allowed to run from the cylinder as the nitrite entered, before the salt solution slowly driven into the bulb from the syringe. By carefully measuring the exact amount of salt solution in the cylinder, a substitution for this by the gas was effected so that the cylinder was practically emptied of solution. The results were very uniform.

Tracing 49.

Contrasted action of methyl and tertiary butyl nitrite on resting muscle. (See protocol.)

Methyl nitrite is the most active of all the nitrites in causing an early initial shortening of the muscle. In from 25 to 50 seconds, according to the dose and temperature, &c., the first indication of rise of the lever is noticed. The substance most nearly approaching it in this respect is the ethyl nitrite, which is, however, distinctly slower. When the contraction has once commenced it progresses rapidly, so that an abrupt rise, reminding one of tertiary amyl and butyl nitrite, is recorded.

Thereafter the rise goes on for a time but it is very gradual. The total shortening produced is less than that occasioned by a similar dose of any nitrite which has been examined under similar conditions. The following experiment will serve to contrast the effect of tertiary amyl nitrite and methyl nitrite. Tracing 49.

Substance.	Dose.	Lever.	Weight.	Temperature.	Time of initial contraction.	Shortening.					
						2 mins.	4 mins.	8 mins.	16 mins.	32 mins.	64 mins.
			grms.	° C.	secs.	mm.	mm.	mm.	mm.	mm.	mm.
Methyl nitrite	4·3 cub. centims. (4·3 cub. centims. of gas = $\frac{1}{32}$ cub. centim. of liquid bulb = 0·0110 grm.; NO_2 = 0·00829 grm.)	×6	7·5	14	43·5	5·5	8	10	11	11·5	
Tertiary amyl nitrite	$\frac{1}{100}$ cub. centim. (= 0·0089 grm.; NO_2 = 0·0035 grm.)	×6	7·5	14	140	0	12	18	20	21	

Contrasted with iso-butyl nitrite, the early part of the methyl curve is much more rapid, whilst the gradual development of the butyl effect causes a slower cutting of the methyl curve, but the characteristic rise above it, so that a dose of $\frac{1}{100}$ cub. centim. of the iso-butyl nitrite far exceeds in 10 minutes the effect of a 9·3 cub. centims. bulb of methyl nitrite equal to $\frac{1}{38}$ cub. centim. Tracing 50.

Tracing 50.

Contrasted action of methyl and iso-butyl nitrite on resting muscle. (See protocol.)

Substance.	Dose.	Lever.	Weight.	Temperature.	Time of initial contraction.	Shortening.					
						2 mins.	4 mins.	8 mins.	16 mins.	30 mins.	60 mins.
			grm.	° C.	secs.	mm.	mm.	mm.	mm.	mm.	mm.
Methyl nitrite	9·3 cub. centims. bulb (= 0·0238 grm.; NO_2 = 0·0179 grm.)	×6	7·5	9·75	43	1·0	14·5	17·5	21	24	29
Iso-butyl nitrite	$\frac{1}{100}$ cub. centim. (= 0·0087 grm.; NO_2 = 0·0038 grm.)	×6	7·5	9·75	126	0	9·5	20·5	31·5	37·5	52

It will be noticed that the application of the iso-butyl nitrite occurs before that of the methyl nitrite in this curve.

The last measurements which will be given contrast the effect of methyl and ethyl nitrites. A large dose of each substance is employed; a 13 cub. centims. bulb of methyl nitrite (= $\frac{1}{27}$ cub. centim.) and $\frac{1}{30}$ cub. centim. ethyl nitrite respectively.

Substance.	Dose.	Lever.	Weight.	Temperature.	Time of initial contraction.	Shortening.					
						1 min.	2 mins.	4 mins.	8 mins.	16 mins.	30 mins.
			grm.	° F.	secs.	mm.	mm.	mm.	mm.	mm.	mm.
Methyl nitrite	13 cub. centims. bulb (= 0·0291 grm.; NO_2 = 0·0219 grm.)	×11	10	54	35	3·5	8	10	11·5	13·5	18
Ethyl nitrite	$\frac{1}{30}$ cub. centim. (= 0·0296 grm.; NO_2 = 0·0182 grm.)	×11	10	54	48	1	5	14·5	20	24	28·5

Having described in detail the action of the various nitrites respectively upon striated muscular tissue, we can now arrange them in series according to—

(*a.*) Their power of causing shortening of resting muscle—
  1. With reference to the extent of this shortening.
  2. With regard to the speed of its occurrence.

(*b.*) Their power of modifying the active contraction of muscle subjected to periodic stimulation.

(*a.*1) The order of activity of the nitrites with reference to the extent of muscular shortening produced is as follows:—

(We consider here the shortening occurring in from 15 minutes to 120 minutes after the introduction of nitrite into the muscle chamber, not the shortening occurring sooner, as this must vary with the speed of initial action of the nitrite, and also with the tendency for a maximal effect for a given dose to be rapidly or slowly produced.)

1. Iso-butyl nitrite.
2. Tertiary amyl „
3. Secondary butyl „
4. „ propyl „
5. Propyl „
6. Tertiary butyl „
7. Butyl „
8. α-Amyl „
9. β- „ „
10. Ethyl „
11. Methyl „

(*α*.2) SPEED of Occurrence of Shortening.

1.	Methyl	nitrite.	
2.	Ethyl	„	
3.	Secondary propyl	„	
4.	Tertiary amyl	„	
5.	Primary propyl	„	nearly equal.
6.	Tertiary butyl	„	
7.	Secondary butyl	„	
8.	*α*-Amyl	„	nearly equal.
9.	*β*- „	„	
10.	Butyl	„	nearly equal.
11.	Iso-butyl	„	

(*b*.) The curve uniting the points from which successive contractions ascend is not strictly parallel with the curve of passive contraction of an unstimulated muscle exposed to a similar amount of an individual nitrite, the weight and temperature being equal. The former is modified by the increased tonus, or after-shortening, of those muscle fibres which are still capable of contracting in response to recurring stimulation as well as of those which are passing, or have already passed into rigor. In the other direction, the extending force of the falling weight (the weights were free, *i.e.*, unsupported) after active contraction tends to elongate the muscular tissue.

We do not propose to enter, at the present time, into a consideration of the part which these factors play in modifying the passive shortening of the muscle, inasmuch as it would not aid us in our present endeavour to separate the nitrites from one another. The abolition of active contraction runs so far parallel with the power of individual nitrites to cause passive shortening, terminating in well-marked rigor of resting muscular tissue, that it may be said, in a word, that these conditions, within certain limits, show a parallel progress to one another. When companion muscles are stimulated in an atmosphere containing nitrite vapour, the muscle which shortens the more powerfully ceases to contract sooner in response to stimulation, provided the initial active contraction was equal in the two cases. If this condition was not fulfilled, divergencies from the usual course were from time to time observable; a feebly contracting muscle, tending to "give in," or cease contracting at an earlier phase of shortening than a powerfully reacting muscle. Experiments of this nature were necessarily discarded. The remaining ones permit us to classify the nitrites with reference to their power of abolishing active contraction in the same order as in Table *α*.1.

It was ascertained that very minute doses of the nitrites, insufficient to cause marked passive shortening, interfered with active contraction, causing the failure of the muscle to respond to stimulation, whilst the companion muscle, in a closed chamber devoid of nitrite vapour, still responded. A comparison of the action of the various nitrites in this respect, which would have involved an additional series of observations to those already made, was not considered of sufficient importance to be undertaken in connection with the present inquiry.

IX.—Discussion of the Mode of Dependence of Physiological Action on Chemical Constitution.

We now proceed to discuss the mode of dependence of the physiological action of the paraffinic nitrites on their molecular composition and structure.

The different phases of physiological action concerning which we have obtained accurate quantitative data are (1) acceleration of the pulse-rate; (2) reduction of the blood-pressure in respect of (*a*) its extent, and (*b*) its duration; (3) contraction of striated muscular fibre in respect of (*a*) its extent, and (*b*) its rate. The quantitative variations in these effects, which follow from the administration of equal volumes of the various nitrites, have been accurately measured.

Several physical and chemical differences in these bodies must be taken into account in correlating physiological action with chemical constitution, and it will be well to state briefly what these are before the action of each is separately considered.

In the first place it must be pointed out that, since equal volumes of the liquid nitrites, measured at 15° C., have been employed in the physiological experiments, and the relative densities of these liquids are not identical, the equal volumes will not represent exactly equal weights. The nitrites of high molecular weight (butyl, amyl) have slightly smaller relative densities than those of low molecular weight (ethyl, propyl), so that, as the same volume of all the nitrites has been taken, the corresponding weights of the lower nitrites will be greater than those of the nitrites which stand higher in the series. These differences in weight, corresponding to the small volumes used in these experiments ($\frac{1}{30}$th to $\frac{1}{200}$th cub. centim.) are, however, relatively very small, and only affect the quantities used in the fourth or fifth decimal place. Thus, if we calculate the weights corresponding to the $\frac{1}{50}$th cub. centim. of the two nitrites which exhibit the greatest differences in their relative densities, ethyl nitrite and tertiary butyl nitrite, the difference between them only amounts to 0·0006 grm., which represents a smaller volume than it would have been practicable to measure under the circumstances of our experiments. Although these differences are so minute it is worth while to take them into account in calculating the weight of nitroxyl (NO_2) contained in equal volumes of the different nitrites, and for this reason in the record of each experiment the weight corresponding to the volume taken has been given within brackets.

Another difference in physical property to which attention must be paid is that in volatility. Ascending the homologous series from ethyl nitrite to amyl nitrite it is observed that the boiling point of the primary compounds increases by almost exactly

30° C. for each addition of CH_2. The tertiary nitrites boil at lower temperatures than the secondary nitrites and these in their turn at lower temperatures than the corresponding primary compounds. With the exception of methyl nitrite, which is a gas, all the nitrites used are liquids at common temperatures. It is conceivable that the more volatile nitrites might act more rapidly than those which are less volatile, whilst the effect produced by the volatile nitrites might be expected to be more transitory than that of the less volatile, and therefore less diffusible compounds.

All the nitrites examined belong to a homologous series the composition of whose members is representable by the general formula $C_nH_{2n+1}NO_2$ from which it follows that as the series is ascended with increase of molecular weight, the amount of nitroxyl contained in each molecule decreases. This fact has an important bearing on the elucidation of the chemical cause of the physiological action of these bodies. For if their physiological activity is conditioned by the presence of the nitroxyl group then this activity should be most powerfully exerted by those compounds which are richest in this constituent, viz., those of low molecular weight, which stand at the commencement of the series; whereas those nitrites which contain proportionately less nitroxyl, viz., those of high molecular weight, which stand last in the series, should be the weakest in their physiological action. That the presence of the nitroxyl group is the principal cause of the characteristic physiological effects of these compounds there can be no doubt, since the inorganic nitrites (sodium and potassium nitrites) have been observed to give rise to many of the phenomena described in the former part of this paper as arising from the administration of organic nitrites. This being so the question to be elucidated is to what extent, and in what manner, do the different alkyl radicals, which in the organic nitrites are joined to nitroxyl, modify its characteristic action. It may happen that these alkyl radicals act in the same physiological direction as nitroxyl, in which case the difference in the power of the lower and higher members of the series would not be so prominent, and, in the event of the activity of these alkyl radicals becoming greater as the series is ascended, might not even be distinguishable. Unfortunately the physiological action of other salts of these alkyl radicals has not been investigated with any great minuteness, although there is recorded evidence that their hydroxides or alcohols, when administered in small doses, lead to an acceleration of the pulse-rate which is also a prominent feature in the action of the nitrites.

Since the different phases of the physiological action of these organic nitrites vary with an increase in molecular weight, and also with the employment of primary, secondary, or tertiary compounds, it will be necessary to consider the constitutional differences which exist in these compounds, to the influence of which the variations in physiological action must be directly or indirectly due. It will be convenient to point out here once and for all in what these differences consist.

The primary nitrites, both normal and iso-primary, differ from the secondary and tertiary compounds in containing nitroxyl joined to a methylene group (CH_2) and all these primary compounds therefore contain the complex (CH_2NO_2) united with different alkyl radicals. In the secondary nitrites one atom of hydrogen in this group is replaced by methyl (CH_3)$CH(CH_3)NO_2$ whilst in the tertiary nitrites both the hydrogen atoms are replaced by methyl, and these bodies therefore contain the group $C(CH_3)_2NO_2$.

The relationships subsisting between the members of this homologous series may be represented most conveniently for the purposes of this discussion by considering each compound as the methyl derivative of that standing immediately below it in the series, and from which it may be regarded as formed by the replacement of an atom of hydrogen by methyl (CH_3 or Me). Thus ethyl nitrite ($CH_2(Me)NO_2$) may be looked upon as the methyl derivative of methyl nitrite (CH_3NO_2), the two propyl nitrites (primary and secondary) as the methyl derivatives of ethyl nitrite; if the methyl group takes the place of an atom of hydrogen in the already existing CH_3 group of this compound we have the primary propyl nitrite ($CH_2CH_2(Me)NO_2$), but if it replaces hydrogen in the methylene (CH_2) group, the secondary propyl nitrite $CH(Me)CH_3NO_2$ or $CH(CH_3)_2NO_2$ results. Similarly the four butyl nitrites (primary, iso-primary, secondary, and tertiary), may be regarded as methyl derivatives of the two propyl nitrites. Primary butyl nitrite ($CH_2CH_2CH_2(Me)NO_2$) results from the introduction of the methyl into the already existing methyl group of primary propyl nitrite; if the radical takes the place of hydrogen in one of the methylene groups, but not in that which is attached to nitroxyl, the iso-primary butyl nitrite ($CH_2CH(Me)CH_3NO_2$) is obtained. In the secondary butyl nitrite ($CH(Me)CH_2CH_3NO_2$) the substituted methyl radical occupies the place of an atom of hydrogen in the CH_2NO_2 group of primary propyl nitrite, whilst in the tertiary butyl nitrite ($C(Me)\ (CH_3)_2NO_2$ or $C(CH_3)_3NO_2$) it takes the place of hydrogen in the $CH\ NO_3$ group of secondary propyl nitrite, and so on.

From this point of view the nitrites with which we have to deal may be systematically arranged as follows, the newly substituted methyl group being represented by the symbol (Me).

Nitrites.	Primary.	Secondary.	Tertiary. *
Methyl CH_3NO_2 .	CH_3NO_2	—	—
Ethyl $C_2H_5NO_2$ . .	$CH_2(Me)NO_2$	—	—
Propyl (2) $C_3H_7NO_2$	$CH_2CH_2(Me)NO_2$	$CH(Me)CH_3NO_2$	—
Butyl (4) $C_4H_9NO_2$.	$CH_2CH_2CH_2(Me)NO_2$(normal) $CH_2CH(Me)CH_3NO_2$(iso-)	$CH(Me)CH_2CH_3NO_2$	$C(Me)(CH_3)_2NO_2$
Amyl (3) $C_5H_{11}NO_2$	$CH_2CH_2CH(Me)CH_3NO_2$(α-iso) $CH_2CH(Me)CH_2CH_3NO_2$ (β-iso)*	—	$C(Me)CH_3CH_2CH_3NO_2$

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* The physiological action of the α-iso-amyl and β-iso-amyl nitrites is so nearly the same, that in this discussion no distinction will be made between them.

All the nitrites of this series suffer decomposition more or less readily, especially when in contact with dilute acids or alkalies. The principal chemical change consists in hydrolysis of the nitrite into nitrous acid, and the corresponding alcohol, in accordance with the equation $R'NO_2 + H_2O = R'OH + HNO_2$; but a number of secondary changes also take place, most of which originate with an oxidation of the alcohol. The nitrites which stand highest in the series, *i.e.*, those of high molecular weight, are the most readily decomposed, whilst the secondary and tertiary bodies suffer decomposition far more easily than primary compounds; and the iso-primary bodies, apparently, are rather more subject to change than the normal compounds. As will subsequently be pointed out, the readiness with which the nitrites suffer decomposition appears to be closely connected with certain phases of their physiological activity. Having now referred to the most important differences in the chemical properties of these nitrites, whose physiological effects have been investigated, we are in position to discuss the connection subsisting between these two classes of phenomena.

Acceleration of the Pulse-Rate.—The acceleration in the rate of the pulse beat is one of the most remarkable effects resulting from the administration of these compounds, either by inhalation or by intra-vascular injection to animals or to man. There is, however, a very marked variation in the power of the different nitrites in this respect. The numerical order corresponding with the increasing powers of these compounds in accelerating the pulse is as follows.* The nitrites are divided into primary, secondary, and tertiary compounds, and the numbers within brackets refer to the general order of activity.

Primary nitrites.	Secondary nitrites.	Tertiary nitrites.
1. Methyl (1) 2. Ethyl (2) 3. Propyl (3) 4. Butyl (normal) (5) 5. Butyl (iso) (7) 6. Amyl (α and β-iso) (9)	1. Propyl (4) 2. Butyl (6)	1. Butyl (8) 2. Amyl (10)

This order is for the most part the same whether the nitrites are administered by inhalation or by intra-vascular injection, and in all the cases examined, as far as they have been tested, holds good for man, as well as for animals. The acceleration resulting from intra-vascular injection is, however, invariably less than that occasioned by inhalation. The nitrites of low molecular weight possess little or no power of accelerating the pulse, and indeed in some cases actually retard it. The order of physiological activity exactly corresponds with that in which these nitrites stand in the homologous series, that is to say, the physiological activity increases with the molecular weight. Contrasting the action of corresponding primary, secondary, and

* In previous tables in the paper the nitrites are arranged in the reverse order, beginning with the most active.

tertiary compounds, the secondary and tertiary nitrites possess the greatest power, the tertiary amyl nitrite being indeed the most active of all the nitrites examined.

If correction is made for the slightly different densities of the liquid nitrites, equal volumes of which have been administered, and equal weights are calculated, it does not disturb the order, since it would favour the nitrites of high molecular weight which already occupy the leading position. The greater volatility and diffusibility of the lower members evidently does not give them an advantage in connection with the action on the pulse.

This order of physiological activity is not in harmony with the view that the action on the pulse is entirely, or even principally conditioned, by the presence of nitroxyl, indeed, the facts as they stand point to exactly the opposite conclusion. A certain volume of ethyl nitrite, which is with one exception the weakest member of the series, represents twice as great a weight of nitroxyl as the same volume of the most active compound, viz., tertiary amyl nitrite, and in general the physiological activity is inversely as the amount of nitroxyl the compound contains.

When the differences in the chemical constitution of these nitrites are taken into account, we are led to the conclusion that either directly or indirectly the methyl, and not the nitroxyl group is the determining cause of activity, since the successive substitution of methyl, which occurs as the series is ascended, is accompanied by an increase in pulse-accelerating power, whilst this introduction of methyl involves a proportionate decrease in the amount of nitroxyl. The superior activity of secondary and tertiary compounds proves that the physiological effect of the substitution of methyl is greatest when it occurs in the hydrogen of the methylene group, which is in direct union with nitroxyl (CH_2NO_2); that is to say, when the methyl group is joined to the carbon atom which is directly united to nitrogen, as in secondary nitrites, the physiological effect is greater than when the methyl group is attached to any one of the carbon atoms not directly united to nitrogen, and the attachment of two methyl groups to this particular carbon atom, which occurs in tertiary compounds, produces a greater physiological effect than the attachment of only one such group.

The influence of methyl in enhancing the physiological action of these bodies being thus certainly demonstrated, the question arises as to whether this influence is direct or indirect. As evidence that the influence may be in part direct, the similar action of the corresponding alcohols may be mentioned. It appears that in small doses the alcohols lead to an acceleration of the pulse, and that their power in this respect increases as the series is ascended, that is to say, with each addition of methyl. The behaviour of the alcohols has not, however, been investigated sufficiently fully to justify us in accepting any conclusion drawn from an apparent analogy between their action and that of the nitrites, unless it is confirmed by independent evidence. We believe that the data we have recorded put beyond question the conclusion that for the most part the effect produced by the introduction of methyl is an indirect one. The progressive increase in molecular weight, which accompanies the successive introduction of methyl, causes a gradual decrease in the chemical stability of the nitrites, the higher nitrites being more susceptible to decomposition than those lower in the series. It is this tendency to decompose, which appears to govern the physiological action of these compounds, those bodies which most readily decompose being the most active, and *vice versâ.* The conclusion that the connection between instability and physiological action is a causal one, receives support from the behaviour of corresponding primary, secondary, and tertiary nitrites. The secondary and tertiary bodies are the most active, and are also the most unstable; in fact, on this account it is very difficult to prepare them, and impossible to retain them in a pure state. Here, again, the great increase in physiological power which attends the attachment of one or two methyl groups to the carbon atom directly bound to nitrogen seems to be principally due, not to the direct physiological influence of the substituted methyl group, but to the chemical instability which the introduction of this group confers on the molecule. What the exact nature of the chemical change is which accompanies the manifestation of the physiological action it is impossible to assert for want of experimental data. It may proceed by way of oxidation or of hydrolysis. GAMGEE ('Phil. Trans.,' 1868, 589), who was the first to study the remarkable change in the colour of arterial blood, from bright red to chocolate brown, which is noticed whenever nitrites are administered, has suggested that it is the result of the formation of a combination of the nitrite with the hæmoglobin. The fact that later observers have shown that the actual colour change is due to the production of methæmoglobin, and may be brought about by substances other than nitrites, has caused this suggestion of GAMGEE, which is strongly supported by his experimental data, to be lost sight of. Our own results have led us to believe that the combination of the nitrites with the hæmoglobin, or with some other constituent of the blood, is very probably the first step in the chemical change which unquestionably occurs when a nitrite is brought into contact with the blood or with muscle. Chemical decomposition, however, doubtless very quickly follows this initial combination, especially with the higher and less stable compounds. Preliminary experiments made with the object of tracing the chemical changes which nitrites undergo in the body have proved that these compounds are eliminated in the urine chiefly as nitrate, since more than two-thirds of the total quantity may be recovered from the urine in this form if certain precautions are taken. Thus whilst in the first chemical change the nitrite probably enters into a loose combination, the final chemical result is oxidation, but where this oxidation takes place, and what the preceding chemical changes are, it is impossible at present to say, except that hydrolysis almost certainly precedes the oxidation. In connection with the conclusion that chemical instability is the property which determines the physiological activity of these nitrites in accelerating the pulse, it is interesting to observe that the behaviour of the lower members of the series which do not so readily decompose leads to the suggestion that *per se* the paraffinic nitrites, at any rate when administered in small doses, do not accelerate but actually retard the pulse-beats, and that acceleration only commences when chemical change has set in. Methyl nitrite, the lowest and most stable member of the series, produces immediately after its administration a great retardation in the beat of the pulse, followed after an interval by a very small acceleration. Ethyl nitrite behaves similarly, the first effect being to retard the pulse-rate, whilst this is followed after a distinct interval by a slight acceleration, greater, however, than that resulting from methyl nitrite. Propyl nitrite produces at first a small retardation, and afterwards a marked acceleration. The nitrites higher in the series than proypl nitrite produce little or no initial retardation, but after the lapse of some seconds considerable acceleration is observed. These peculiarities are quite in harmony with the view expressed above. The action of small quantities of the unaltered nitrites, which is most prominent in the case of the lower stable members, is to retard the pulse; but after a definite interval, when decomposition has commenced, an acceleration more or less rapidly ensues, being most marked in the case of the highest and least stable members of the series.

Reduction of the Blood-Pressure.—In this prominent physiological effect of the administration of the nitrites we have a more complicated problem to unravel than the action on the pulse. It has already been remarked, in the first part of this paper, that evidence has been obtained which goes to show that the pulse acceleration cannot be regarded as wholly due to the fall in blood-pressure, and that the two results must be considered to some extent as distinct.

In discussing the action of the various nitrites on blood-pressure we have to distinguish between the extent of the reduction and the time during which it lasts, since the nitrites which give rise to the greatest fall, are not identical with those whose action is most prolonged.

The following is the order corresponding with the increasing power of the various nitrites with reference to the extent to which they reduce the normal pressure of the blood :—

Primary nitrites.	Secondary nitrites.	Tertiary nitrites.
1. Propyl (1) 2. Ethyl (2) 3. Butyl (3) 4. Methyl (4) 5. Amyl (5) 6. Iso-butyl (7)	1. Propyl (10) 2. Butyl (8)	1. Butyl (9) 2. Amyl (6)

This order is generally the same as that for pulse acceleration. The secondary and tertiary nitrites and, after them, the iso-primary nitrites of amyl and butyl stand highest, and are more active than the normal primary compounds. In general the power of reducing blood-pressure increases with molecular weight, but there are several exceptions to the rule, notably in the case of methyl nitrite, which occupies a higher position as a pressure reducing agent than it does as a pulse accelerator.

If correction is made for the difference in the densities of these liquids the position of some of the nitrites of small molecular weight would probably be lowered, and a nearer approximation obtained to an order corresponding with that of the homologous series.

It is, however, remarkable that in most cases an increase in the quantity of nitrites administered does not lead to the corresponding increase in the reduction of blood-pressure which we should expect, in fact the relatively powerful action of small quantities of these compounds is very extraordinary.

The differences in the boiling-points of the liquids do not seem to exercise any important influence on the extent to which they reduce blood-pressure. Those boiling at lower temperatures do not act more rapidly.

The amount of nitroxyl present in the compound evidently does not here, any more than in the action of the pulse, condition the physiological activity. The tertiary butyl and amyl nitrites, though containing much less nitroxyl than the nitrites of ethyl and propyl, are the most active. With certain exceptions the power of reducing blood-pressure increases with the molecular weight, and, therefore, with the introduction of the methyl group. The conclusion arrived at in connection with the similar though more regular relationship of the methyl radical to the power of accelerating the pulse is evidently also applicable here. The determining cause of the reduction of blood-pressure is the chemical instability of the higher members of the series, and especially of the secondary and tertiary compounds. There is no recorded evidence to show that the increase in activity is the result of the direct physiological influence of the methyl group.

As we know next to nothing about the nature of the chemical changes which accompany the reduction of blood-pressure, it is not possible to discuss this relationship any more fully on its chemical side than was done in connection with pulse acceleration, and for the same reason it is not possible to offer any satisfactory explanation of the irregularities which the table discloses in the behaviour of some of these compounds.

The results taken as the basis of the foregoing discussion of the experiments on blood-pressure were obtained by administering equal volumes of the liquids by inhalation. When these compounds are given by intra-vascular injection they produce a similar effect, and in general there can be no doubt that the action results from the same cause.

As regards duration of the sub-normal pressure the order of increase is as follows :—

Primary nitrites.	Secondary nitrites.	Tertiary nitrites.
1. Propyl (1) 2. Iso-butyl (3) 3. Amyl (4) 4. Butyl (5) 5. Ethyl (9) 6. Methyl (10)	1. Propyl (2) 2. Butyl (6)	1. Butyl (7) 2. Amyl (8)

The relatively small reduction of pressure effected by the primary nitrites of ethyl and methyl lasts longer than that produced by any other nitrite, even by those having the highest molecular weights whose power of reducing pressure is very considerable. In most cases it appears that those nitrites which occasion the most extensive fall in blood-pressure act for the shortest time, and *vice versâ*. The most important exception to this statement is found in the action of primary propyl nitrite which is the weakest member of the series both in respect of the extent to which it reduces blood-pressure and also in the duration of its action. In duration, as well as in extent of reduction, secondary and tertiary nitrites are more powerful than the corresponding primary compounds; secondary propyl nitrite is stronger than primary propyl nitrite, secondary butyl nitrite is stronger than primary butyl nitrite, tertiary butyl nitrite is more active than either the primary or secondary compounds, and tertiary amyl nitrite is more active than iso-primary amyl nitrite.

It does not appear that the correction for the differences in density of the liquid nitrites would materially affect the order given above for equal volumes, since unless the quantity administered is very largely increased, the duration of subnormal pressure is not affected to any great extent.

The difference in the volatility of the various nitrites does not appear to operate in the direction that might be expected, since the action of two of the most volatile and readily diffusible compounds is the most prolonged.

In its relation to molecular composition the greatest duration of subnormal pressure is in general associated with low molecular weight, and, therefore, with those compounds which contain a proportionately large amount of nitroxyl. It is, however, not safe to conclude that the quantity of nitroxyl is the direct and only cause of the permanence of the action on blood-pressure. If it were the direct cause it would follow that a great increase would result from the administration of slightly larger quantities, which is not the case; the duration of subnormal pressure, though greater when larger quantities of the nitrites are administered, falls very far short of being proportionately greater. That the quantity of nitroxyl is not the only factor in the permanence of this physiological effect is clear from the circumstance that, whilst iso-primary amyl nitrite represents almost exactly the same amount of nitroxyl as tertiary amyl nitrite, the latter is much the more powerful compound. The fact that the most volatile and diffusible nitrites (methyl and ethyl nitrites) act for the longest time, is in accordance with the view that these compounds at first attach themselves to some constituent of blood or muscle, and are, therefore, only slowly eliminated. The nitrites of high molecular weight would less readily enter into combination, and, being more unstable, would be more quickly decomposed ; and thus these effects would last for a shorter time than those of the more stable compounds of lower molecular weight.

It is not possible in the present state of our knowledge to offer a complete chemical explanation of the peculiarities in the behaviour of these nitrites in reducing blood-pressure. There can, however, be no doubt that whilst the causes which lead to the acceleration of the pulse and the reduction of pressure are essentially the same, those which control the duration of subnormal pressure are distinct ; the first-mentioned effects are associated with molecular instability, whilst the latter effect, in its intensest form, is produced by the most stable compounds of the series.

Contraction of Striated Muscular Fibre.—In examining the action of equal volumes of the nitrites on striated muscle, there were observed to be two distinct aspects of this action, which invariably leads to passive muscular contraction. One relates to the extent to which the contraction takes place, and the other to the rapidity with which it occurs. These two manifestations of power are not associated with the same nitrites. Considering first the extent of the contraction, the order representing the increasing power of the various nitrites in this respect is as follows :—

Primary nitrites.	Secondary nitrites.	Tertiary nitrites.
1. Methyl (1)	1. Propyl (7)	1. Butyl (5)
2. Ethyl (2)	2. Butyl (8)	2. Amyl (9)
3. Amyl (3)		
4. Butyl (4)		
5. Propyl (6)		
6. Iso-butyl (10)		

This order presents many similarities with that for extent of reduction of blood-pressure. The secondary and tertiary nitrites are again the most active compounds with the exception of iso-butyl nitrite, which acts more powerfully than any other member of the series. The nitrites of methyl and ethyl are the least efficient in producing muscular contraction.

It does not appear that the order for equal weights of the nitrites would differ in any important respect from that given above for equal volumes. It is difficult to determine how far the differences in the volatility of the various nitrites are connected with the differences in this physiological action. The two most volatile compounds, methyl and ethyl nitrites, are certainly the weakest, whilst iso-butyl nitrite, which is one of the least volatile compounds, is the strongest in its action. On the other hand, the more volatile propyl nitrites are far more active than the much less volatile iso-primary amyl nitrite, which is one of the weakest members of the series. It is clear that volatility is not the most important of the factors which lead to the modification in physiological action. Although there are certain well marked irregularities in the order, if we have regard to the strongest nitrites, viz., those of iso-butyl, tertiary amyl, and secondary butyl, and to the weakest compounds, viz., the nitrites of methyl and ethyl, it appears that, for the most part, the power of contracting muscular fibre is associated with high molecular weight, and is not conditioned by the quantity of nitroxyl which the nitrite contains.

Iso-butyl nitrite, the strongest member of the series, represents less than half the quantity of nitroxyl contained in an equal weight of methyl nitrite, which is the weakest of all the compounds. This fact, taken in conjunction with the high place occupied by the secondary and tertiary compounds, points to the conclusion that chemical instability is here again the principal determining condition of physiological activity.

In relation to the rapidity with which muscular contraction is effected as distinguished from its extent, quite different nitrites prove themselves to be the most efficient. The order in which the nitrites are arranged, according to the increasing rate at which they produce muscular contraction, is as follows:—

Primary nitrites.	Secondary nitrites.	Tertiary nitrites.
1. Iso-butyl (1) 2. Butyl (2) 3. Amyl (3) 4. Propyl (6) 5. Ethyl (9) 6. Methyl (10)	1. Butyl (4) 2. Propyl (8)	1. Butyl (5) 2. Amyl (7)

This order shows some irregularities, but, as far as the quickest and slowest acting nitrites are concerned, it is exactly the reverse of that representing the extent to which contraction is brought about. Iso-butyl nitrite, which causes a greater muscular contraction than any other nitrite, is the slowest in acting, whilst the nitrites of methyl and ethyl, which give rise to the least considerable contraction, are quickest in their action. Among the exceptions attention must be drawn to the remarkable position occupied by the secondary and tertiary nitrites, which is but very slightly inferior to that which they hold in respect to extent of contraction; in all cases the secondary compounds act quicker than the corresponding primary compounds; secondary propyl and butyl nitrites start the contraction before primary propyl and butyl nitrites, whilst tertiary amyl nitrite acts considerably quicker than the iso-primary compound.

The respective positions of these nitrites would not be materially altered if the order were taken for equal weights instead of equal volumes.

The more volatile compounds in many instances act most rapidly, *e.g.*, methyl and ethyl nitrites; but there are numerous exceptions, whilst the differences in the boiling-points of iso-primary and tertiary nitrites, and of iso-butyl nitrite and secondary and tertiary butyl nitrites, are too small to account for the far greater activity of the secondary and tertiary compounds.

In the case of the three most active primary nitrites, viz., those of propyl, ethyl, and methyl, the order of their activity is the reverse of the homologous order, and is therefore inversely as their molecular weights. The three primary nitrites which act most slowly are those of high molecular weight, viz., iso-butyl, butyl, and amyl nitrites. It therefore appears that, as far as the primary compounds are concerned, speed of action is associated with low molecular weight, and therefore with a large proportion of nitroxyl. No doubt the greater volatility which accompanies low molecular weight may also assist the rapid action of these nitrites.

A study of the behaviour of the secondary and tertiary nitrites leads to the conclusion that in these compounds the two factors of low molecular weight, or large nitroxyl content, and volatility, are not alone sufficient to account for the presence of these compounds among the more active members of the series. Between corresponding primary and secondary nitrites there is a considerable difference in speed of action, although there is no difference in molecular weight, and relatively only a small variation in boiling-point. The greater activity of the secondary and tertiary compounds must therefore be attributed to peculiarities in their constitution. These bodies differ from the primary compounds in containing one or two methyl groups attached to the carbon atom which is combined with nitroxyl. It may safely be concluded that the superior activity is not the result of the direct physiological influence of the methyl groups, but to the chemical instability induced by their presence in this part of the molecule, which causes these compounds to be the most readily decomposed of all the nitrites of this series.

We find then, in respect of the speed with which muscular contraction occurs, that first the primary nitrites of low molecular weight, and then the secondary and tertiary nitrites of high molecular weight, are the most active members of the series, whilst the primary nitrites of high molecular weight stand last, in being the slowest in starting muscular contraction. The question at once suggests itself as to why these two widely separated sections of the series should correspond in the rapidity of their physiological action. It has already been pointed out, in connection with the action on blood-pressure, that all the nitrites probably act in the first instance by entering into a loose combination with one of the constituents of the blood, and that the nitrites of low molecular weight no doubt do so the most readily. The results we have obtained with muscle point to a similar conclusion. If the nitrites combine with one of the constituents of muscle, those of low molecular weight entering more readily into combination than those of high molecular weight, the difference in the speed with which the various primary nitrites act becomes, at least, intelligible. As regards the behaviour of the secondary and tertiary compounds, it is highly probable that, on account of their great instability, they would at once undergo hydrolysis on coming into contact with the acid of actively contracting muscle, and that the separated nitrous acid would then immediately react. The slowness with which the nitrites of high molecular weight act may be ascribed to the circumstances that these bodies enter much less readily into combination, and are far more stable than the secondary and tertiary compounds. The weak chemical union between the nitrites and certain constituents of blood and muscle, of which their physiological action affords indications, although substantiated to some extent as regards the blood by the experiments of GAMGEE, requires detailed chemical study with respect to the nature of the compound, as well as to its modes of decomposition.

In conclusion, the following are the principal facts which have been established with reference to the connection between the various phases of the physiological action of these nitrites and their chemical constitution.

In respect of all phases of the physiological action, the secondary and tertiary nitrites are more active than the corresponding primary compounds. This is to be chiefly attributed, not to the direct physiological effect of the secondary and tertiary groups, but to the great facility with which these compounds suffer decomposition.

In respect of the acceleration of the pulse, the power of the nitrites varies directly as their molecular weights, and they therefore fall into an order identical with that of the homologous series. This same relationship, increase of activity corresponding with rise in molecular weight, may also be traced, though less uniformly, in their power of reducing blood-pressure and of inducing muscular contraction.

This order appears to be the result, not so much of the direct influence of the substituted methyl groups, as of the increased chemical instability which their substitution confers on the higher members of the series.

In respect of the duration of sub-normal pressure, as well as of the rapidity with which muscular contraction ensues, the activity of the nitrites is expressed by an order which is for the most part the reverse of that representing their power in accelerating the pulse, reducing blood-pressure, and contracting muscular fibre, this order being in general contrary to that of the homologous series. In these respects the more volatile nitrites of low molecular weight, and containing, therefore, relatively more nitroxyl, are the most active. It is probable that these simple nitrites more readily attach themselves to constituents of blood and muscle, and thus act more quickly than the higher compounds in inducing muscular contraction, whilst their greater stability causes their effect, *i.e.*, reduction of blood-pressure, to endure for a greater length of time than that of the higher and more easily decomposed bodies.

It is obvious that these results have an important bearing on the therapeutic employment of the nitrites, which in recent years has become more and more extensive. We propose elsewhere to consider what the outcome of this investigation is for practical medicine.

IX. *Experiments in Examination of the Peripheral Distribution of the Fibres of the Posterior Roots of some Spinal Nerves.*

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[PLATES 42–52.]

As a step preliminary to some observations on the reflex functions of the spinal cord of the Monkey, I have attempted to make a rather detailed examination of the distribution of the efferent and afferent roots of each spinal nerve, especially in the lower half of the body of that animal. I have recently published some experimental notes on the arrangement of some motor fibres in the lumbo-sacral plexus, and the present paper deals chiefly with the distribution of the afferent fibres of the roots.

PREVIOUS OBSERVATIONS.

In the researches which have had for their subject the peripheral distribution of the posterior roots of the spinal nerves, the plexuses of the Mammalian fore limb have been more studied than have those pertaining to the hind limb. With the exception of the five experiments extant by L. TÜRCK (1856), there seem no experiments on the cutaneous fields of the afferent spinal roots of the Mammalian hind limb previous to my own. This fact may lend interest to observations, especially on so high a type as the Monkey, and I take this opportunity of expressing my thanks to the Royal Society for pecuniary aid, placing that somewhat expensive laboratory animal within my reach.

Experimental inquiry into the subject appears to commence with C. ECKHARD (1)*, who appended to a research on the innervation of the muscles and movements of the hind limb of the Frog (1849) a brief note on the cutaneous distribution of the sensory roots of the four hindmost spinal nerves of that type. One general conclusion he drew, and it is as follows: "The field of skin to which a sensory root goes is not exactly that which overlies the muscles which are supplied by the corresponding motor root." **Eckhard** cut the posterior roots only, and in the spinal canal; he divided all the roots of the region except the one whose field he wished to examine. The Frog was decapitated. Mechanical stimulation of the skin was employed, and the presence or absence of resulting movement taken as index.

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* The number refers to the number in the list of Literature of the Subject. See p. 647.

Four years later a second research on the subject appeared again from **Ludwig**'s Laboratory in Zurich, by **Peyer** (2). The Vth, VIth, VIIth, and VIIIth cervical and the Ist thoracic spinal nerves were investigated in the Rabbit. **Peyer**'s method consisted in applying mechanical and thermal stimuli to the skin after section of all these nerves except the one under examination. The animal was narcotized by intravenous injection of opium. The spinal canal was not opened and the mixed spinal nerve was divided outside the vertebral column; it is important to note this because it is not easy to ensure *complete* section of the whole sensory root of the nerve outside the canal, and because by the section so performed the reflex will suffer by division of the motor part of the nerve as well as of the sensory.

Peyer's results may be epitomized as follows:—

The Vth cervical nerve receives sensory fibres from the skin of the front and inner side of the shoulder joint, and, from the lower and outer region of the neck as high as midway between the shoulder and the lower jaw.

The VIth cervical nerve receives sensory fibres from the skin of the front of the upper arm as far as its lower third; from the skin over the top of the m. anconæus externus and longus as far as the scapula; from the outer aspect of the shoulder, and the insertion of the m. lat. pectoris.

The VIIth cervical nerve receives sensory fibres from the skin of the front of the forearm as low as halfway to the wrist, from the flexure of the elbow, from the skin over the lower part of the m. anconæus long. as far as the olecranon; from the inner side of the upper arm and forearm, and from the thumb and 2nd digit, and corresponding edge of the manus and wrist.

The VIIIth cervical nerve receives sensory fibres from the skin of the outer side of the forearm, from the volar aspect of the manus, the 5th digit, and the volar and lateral aspects of the 2nd, 3rd, and 4th digits.

The Ist thoracic nerve receives sensory fibres from the back of the forearm, from outer side of the manus up to the middle line of the manus, and from the dorsal and volar aspects of the 3rd, 4th, and 5th digits.

Peyer concluded that in the skin of the limb the fields of the individual spinal nerves more or less overlap each other.

In 1865, W. **Krause** (4), published an investigation into the distribution of the nerves of the fore limb. He used partly the reflex method and partly followed the degeneration of nerve-fibres after section of the nerves. In the Rabbit he found that section of the Vth and VIth cervical nerves did not cause degeneration in any of the finger nerves The VIIth cervical was not tested by degeneration, but **Krause** concluded from the [illegible] that it does not, as **Peyer** had stated, supply the finger and thumb.

KRAUSE stated that just as with the motor roots so also with the sensory, the parts nearest the hand are supplied by the brachial roots lying furthest from the head-end of the cord. He stated of the Ist thoracic and VIIIth cervical roots that their distribution in the skin is so arranged that the VIIIth supplies the radial side of the hand, the Ist the ulnar side, and that the skin fields of the two are separated by a sharp line, running from the tip of the 4th digit. He also stated that each myelinated nerve-fibre contained in a spinal nerve-root stands in fixed relation with a definite anatomical point of the periphery, which point is in all individuals the same. He stated as VOIGT had (8), that variation affects only the course of the fibres between the centre and the periphery, the terminations themselves central and peripheral, remaining invariable. This important conclusion, which contradicts the observation by C. ECKHARD, is certainly erroneous for the motor roots. KRAUSE also stated "that a muscle is supplied with nerve-fibres by the same spinal nerve that innervates the skin overlying it." And this statement controverts the previous one by ECKHARD quoted above. KRAUSE employed for one experiment a Monkey (*Cynomolgus*). He severed the trunk formed by the VIth and VIIth cervical roots, and found in 14 days time no degeneration in the digital nerves of the hand.

In 1868, KOSCHEWNIKOFF (5), examined the cutaneous distribution of the spinal nerves to the hind limb of the Frog, and his results agree well with those recorded in the note by ECKHARD. He found that the fields of distribution of the nerve-roots vary somewhat in different individuals. The VIIth root supplies the outer half of the thigh, knee, and top of the leg. The VIIIth root supplies the inner half of the thigh, the outer part of the knee, the calf, and the whole of the foot. The IXth root supplies the inner side of the thigh, the ham, the inner side of the leg, and the whole of the foot. The skin in most regions of the limb is supplied therefore by two nerve-roots. KOSCHEWNIKOFF used the "reflex" method as ECKHARD had done.

The next research was by C. MEYER (6) and based entirely on the degeneration method. In five Frogs the VIIIth spinal nerve, in three Frogs the IXth spinal nerve was severed, *outside the spinal canal, and the degeneration in the peripheral* nerves resulting after an interval of about 100 days was studied by the microscope. MEYER'S conclusion is that "in the hind limb of the Frog the territories of the VIIIth and IXth spinal nerves are not so exactly and sharply limited as has been shown by KRAUSE to be the case with the two lowest spinal nerves of the brachial plexus of the Rabbit."

The most important work on the distribution of the posterior spinal nerve roots to the skin is that by TÜRCK. His results have suffered from the circumstances of their publication. In 1856, his work had advanced so far that he was able to issue a preliminary account of them in that year (3), but after that time the calls of his professional career were so great that at his death he left the research unpublished and still incomplete. Two years after his preliminary account had been given, the conclusions stated in it were largely incorporated in LUDWIG'S 'Handbuch der Physiologie'

(2nd edition), and two figures are there given in illustration of them. After TÜRCK's death the papers and drawings pertaining to his research were collected and published in 1868 as a *Denkschrift* (7). This posthumous issue was edited by C. WEDL. Much of it is difficult to understand, but the minute care obvious in the fragments will be recognized by anyone who turns to them for reference. The scale on which the work was projected can be gathered from the fact that at TÜRCK's death written records, illustrated in most instances by drawings and by *post-mortem* notes, of more than 350 clinical cases bearing on the question came into the hands of the late Professor DUCHEK. TÜRCK experimented only on the Dog. He divided the spinal nerves outside the vertebral column and, conversely to PEYER, ECKHARD, and KOSCHEWNIKOFF, severed only the spinal nerve which he desired to examine. He tested the sensibility of the skin by pinching it. The number of TÜRCK's experiments extant in the posthumous paper is twenty-five. Of this number twenty were upon the brachial plexus; the remaining five upon the lumbo-sacral. The difficulty of understanding the experimental notes and the drawings left by TÜRCK is partly due to their brevity and to the variation found in different individuals. Partly it is due to the terminology which he considered it advantageous to employ. I will quote his inductions before epitomizing his facts, in order that his terminology may be clearer. He does not appear to have examined the trunk apart from the region abutting on the limbs.

The area of distribution of each nerve-root in the neck and trunk is shaped like a band which runs round from the vertebral column to the ventral middle line in a direction at right angles to the long axis of the body. The areas of distribution of the spinal nerves supplying the skin of the extremities follow, with some modification, the same plan as the other spinal nerves. Their agreement with the others is, however, only apparent when the limbs are brought into a certain position with relation to the trunk. For the anterior extremity this position is when the limb is at right angles to the trunk, fully extended at all its joints and with the hand somewhat supine. The areas of distribution of the limbs behave as if they originally ran round the sides, as in the neck and trunk, and had been displaced by the sideward extension of the limb. Some that have remained attached to the middle lines have been ruptured across, *e.g.*, the IInd and IIIrd thoracic areas. Each spinal nerve has an area of skin belonging to it which is supplied by it *exclusively;* many of the spinal nerves have besides a field of skin exclusively their own, a field which they, in *common* with some other spinal nerves, supply. The nerves of the extremities have no exclusive areas, but only common ones. The nerves of the neck and trunk have very large exclusive areas and very small common areas; it is questionable whether some have any common areas at all.

As TÜRCK's details are important and not very well known, I will abstract them [illegible] at some length.

[illegible] *Cervical Nerve of the Dog.*—Anterior border: from the back of the occiput to midway between the sternal notch and the cricoid. Posterior border: from the VIth cervical spinous process to the sternal notch.

Area of the Vth Cervical of the Dog.—Posterior border: from the Ist thoracic spinous process to the top of the sternum, passing over the supraspinous fossa of the scapula and the point of the shoulder.

Area of the VIth Cervical of the Dog.—Exclusive area: bounded above by the area of the Vth, and stretching under the extensor side of the shoulder joint to end in a narrow point some distance above the flexure of the elbow. Common area with VIIth.

Area of the VIIth Cervical of the Dog.—No exclusive area. Common area with VIth and VIIIth. Touches the lower border of the area of the Vth above on the scapula, and passes below the exclusive area of the VIth, spreading over the middle part of the outer face of the upper arm, and over the outer face of the elbow, the radial side and part of the inner surface of the wrist, thumb, and first phalanx of the 2nd, 3rd, and 4th digits. The upper part of this area is common to VIth and VIIth, the lower to VIIth and VIIIth.

Area of the VIIIth Cervical of the Dog.—No exclusive area. Three common areas: α, with VIIth (above described); β, with Ist thoracic; γ, with VIIth and Ist. Area β extends along the ulnar side of the outer surface of the forearm, wrist, and metacarpus; it includes the 5th digit, the web between the 4th and 5th digits, the outer side of the volar face of the 5th digit, and the outer third of the thenar eminence. Area γ lies between α and β. It includes the middle of the palm and the upper part of the outer side of the forearm.

Area of the Ist Thoracic Nerve of the Dog.—In addition to the above described common areas it has an exclusive area, which extends along the ulnar side of the forearm to near the wrist, and includes the inner condyle.

Area of the IInd Thoracic of the Dog.—No common areas, but two exclusive areas detached one from the other, α and β. Area α, from the 2nd thoracic vertebra over the end of the infraspinous fossa, and then as a band over the thorax and along the outer fold of the axilla to the back of the upper arm and down to the elbow. Area β, a rectangular patch over the 2nd costal cartilage.

Area of the IIIrd Thoracic of the Dog.—No common areas, but two exclusive areas detached one from the other, α and β. Area α, from the 3rd and 4th vertebræ across the back, down the posterior face of the upper arm nearly to the elbow; then over the upper part of the axilla and round the chest. Area β, a patch on sternum at the 4th costal cartilage.

Area of the IVth Thoracic of the Dog to the XIIIth inclusive.—Band-like areas round the body.

Area of the Three Highest Lumbar Nerves of the Dog.—Is a band-like strip extending from the lower edge of the area of the XIIIth thoracic to half-way down the iliac crest behind. It sweeps from not quite up to the middle line of the back to extend toward the middle line of the hypogastric region, but falls short of it, the IIIrd falling farther short than IInd, the IInd than Ist.

Area of the IVth Lumbar of the Dog.—A broad strip from the lower half of the sacrum over the trochanter major down the outside of the thigh round the knee, up the inner side of the thigh, upwards to the abdomen, so as to include the skin of half the penis, but not of the prepuce.

Area of the Vth Lumbar of the Dog.—Has an *exclusive* area, which covers part of the outer side of the knee, the inner side of the leg to below the inner side of the ankle, but barely reaching the inner border of the leg. Has also an area in common with the VIth lumbar, which includes the flexor aspect of the ankle, the back of the foot to the 1st digit, and the inner edge of the foot.

Area of the VIth Lumbar of the Dog.—Has no exclusive area, but two common areas, α (in common with VIIth lumbar), from below the knee narrowing down the outer side of the leg, and over the front of the ankle to the dorsal aspect of the toes. β (in common with Vth lumbar), described under Vth.

Area of the VIIth Lumbar of the Dog.—Has no exclusive area, but two common areas, α (in common with VIth), described above. β (in common with Ist sacral), from the ham to the sole, passing over the outer side of the ankle.

Area of the Ist Sacral of the Dog.—(No written description is extant in TÜRCK's papers, but from the sketches it has a common area (with VIIth), and an exclusive area on the outer surface of the thigh.

Area of the IInd Sacral of the Dog.—Extends from the middle line of the perinæum, not, however, reaching the root of the tail or the anus, round the scrotum or vulva.

Area of the IIIrd Sacral of the Dog.—An area at the side of the root of the tail, including posteriorly the anterior border of the anal orifice.

Area of the IVth Sacral of the Dog.—Smaller than IIIrd, and including the posterior part of the anus.

When we remember the importance of this research, and that it was first published nearly forty years ago, it appears remarkable that its results are not more a part of our common anatomical knowledge than they are.

A paper by HERRINGHAM (10) in 1887 is an important contribution to knowledge on the present subject, although it deals by dissection with the upper limb and not with the limb which is the subject of this paper. Of the details furnished by HERRINGHAM concerning the root-composition of the nerves of the hand I must postpone mention to a paper I hope to publish shortly on the sensory roots of the upper limb. They are chiefly interesting here because they do not confirm the conclusions put forward in KRAUSE's above-mentioned research. Concerning HERRINGHAM's "law," "that any given fibre may alter its position relative to the vertebral column, but will maintain its position relative to other fibres," I have, in a recent paper, drawn attention to the importance and correctness of this law as regards the motor supply to the musculature of the limbs. Concerning the sensory spinal roots and the upper limb HERRINGHAM formulated two rules; "Of two spots on the skin, that which is nearer the preaxial border tends to be supplied by the higher nerve." "Of two spots in the preaxial area the lower tends to be supplied by the lower nerve, and of two spots in the postaxial area the lower tends to be supplied by the higher nerve." These important inductions agree with the arrangement discovered by TÜRCK, and are the more corroborative because HERRINGHAM was apparently unacquainted with the results obtained by TÜRCK.

Concerning the clinical observations elucidating the localizations of the sensory fibres of the spinal segments I regret I can here only briefly refer to them. A valuable collection of them exists in THORBURN's "Surgery of the Spinal Cord" (17), and in the recent paper by ALLEN STARR (18), founded partly upon his own observation and clinique. An important clinical contribution toward an interesting aspect of the subject has been still more lately made by J. MACKENZIE (19) in his 'Sensory Symptoms associated with Visceral Disease.' In the present month Dr. H. HEAD (20) has communicated to the Neurological Society of London an able paper illustrating the topography of pains, referred to the cutaneous fields of the spinal segments in consequence of visceral irritation, and often as features of functional disease. A glance at the figures furnished by these observers suffices to show more than a mere general correspondence between the skin-fields revealed in Man to clinical observation and those of *Macacus rhesus*, the subject of this paper. I think there is little doubt that a close correspondence between the Human lumbo-sacral plexus and that of *Macacus* exists upon the following basis :—*

Macacus rhesus.	Man.
IInd lumbar	Ist lumbar
IIIrd „	IInd „
IVth „	IIIrd „
Vth „	IVth „
VIth „	Vth „
VIIth „	Ist sacral
Ist sacral	IInd „
IInd „	IIIrd „
IIIrd „	IVth „

Before concluding these remarks mention must be made of the luminous essay by Ross (16) " On the Segmental Arrangement of Sensory Disorders." Brief and largely devoted to theoretical considerations as it is, that essay will probably live to be considered the germ of much future research on lines indicated by the suggestions it contains. Its author, like FÉRÉ (9) and HERRINGHAM (10), was evidently unaware of TÜRCK's results, and had he been aware of them the details of his scheme of cutaneous segmentation would doubtless have approached accuracy even more nearly than it does. A salient merit of the essay seems to me the boldness with which to clinical observation it applies the fundamental generalizations obtained by PATERSON (11, 12, 13, 14) from embryological inquiry and from study of the limb plexus in its development.

LITERATURE OF THE SUBJECT.

Experimental.

1. 1849. C. ECKHARD. Zeitsch. f. rationelle Medizin, 1st series, vol. 7, p. 281.
2. 1853. J. PEYER. Arch. f. rationelle Medicin, 2nd series, vol. 4, p. 67.
3. 1856. L. TÜRCK. Vorläufige Ergebnisse, &c. Sitz. d. k. k. Akad. der Wissenschaften z. Wien, p. 586.
4. 1865. W. KRAUSE. Beiträge z. Neurol. d. oberen Extremität. Leipzig.
5. 1868. A. KOSCHEWNIKOFF. Arch. f. Anatomie u. Physiologie. Berlin, p. 326.
6. 1869. C. MEYER. Zeits. f. rat. Med., 3rd series, vol 36, p. 164.
7. 1869. L. TÜRCK. Denkschrift der Wien. Akad., vol. 29.

Morphological.

8. 1864. C. VOIGT. Denkschriften d. Wiener Akad., vol. 22, pp. 1–40.

---

* SHERRINGTON. "Notes on the Arrangement of some Motor Fibres in the Lumbo-Sacral Plexus," Journal of Physiology, vol. 13, 764.

9. 1886. C. Féré. Traité d'Anatomie Médicale du Systôme Nerveux. Paris.

10. 1887. W. P. Herringham. Proceed. of the Royal Society, vol. 41, p. 440.

11. 1887. A. M. Paterson. The Limb-plexuses of Mammals. Jnl. of Anat. and Physiology, vol. 21, p. 611.

12. 1887. A. M. Paterson. On the Functions of the Muscle-plate and the Development of the Spinal Nerves and Limb-plexuses, &c. Jnl. of Micros. Anat., vol. 28, p. 109.

13. 1887. A. M. Paterson. The Morphology of the Sacral Plexus in Man. Jnl. of Anat. and Physiology, vol. 21. Reprinted with additional note. Studies in Anatomy. Owens College, 1891.

14. 1889. A. M. Paterson. The position of the Mammalian Limb. Jnl. of Anat. and Physiol., vol. 23.

21. 1892. P. Eisler. Der Plexus lumbosacralis des Menschen. Halle.

Clinical (the chief and more recent only are given).

15. 1887. W. Thorburn. On Injuries of the Cauda Equina. Brain, vol. 10, p., 381.

16. 1888. J. Ross. The Segmental Distribution of Sensory Disorders. Brain, vol. 10, p. 333.

17. 1889. W. Thorburn. The Surgery of the Spinal Cord. London.*

18. 1892. M. Allen Starr. Local Anæsthesia as a Guide to the Diagnosis of Lesions of the Lower Spinal Cord. Internat. Jnl. of Med. Sci. July.

19. 1892. J. Mackenzie. Sensory Symptoms associated with visceral Disease. The Medical Chronicle. August.

20. 1892. H. Head. On Disturbances of Sensation with especial Reference to the Pain of visceral Disease. Read before the Neurological Society of London, November 10.†

Frog (*R. temporaria*).

The method of investigation employed on the Frog has been as follows :—

Summer Frogs were used. When the animal had been chloroformed under a bell jar, the cerebral hemispheres were carefully exposed through a small trepan hole (Pasteur's 3 millim. trephine), the centre of which lay in the median line. The hemispheres were then completely removed, hæmorrhage being avoided by not using the scissors too freely at the lateral borders. The lowest vertebræ were then exposed and rather completely cleaned of overlying tissue ; one point of a strong though small pair of scissors was then inserted carefully under the left edge of the last vertebra but one, and the lamina cut. The rest, as far as required, were then easily divided by extending the incision, and then the right-hand side (that of the nerve-roots used) was proceeded with. In fact the procedure was that described by C. ECKHARD (1). In one experiment a short incision parallel to the coccyx was made, exposing the four lowest nerves outside the canal, and then all but the desired one was divided. This method, that used by C. MEYER (6), has the disadvantage of not insuring possible twigs of communication between nerve and nerve proximal to the point of section. Further, for my purpose, it limited the field of reply by unnecessary section of the motor roots. In the spinal canal the afferent roots only were divided, and of them, all but the one immediate under examination.

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* Also the Jacksonian Essay, 1892.

† Published in 'Brain,' vol. 16, p. 1, May, 1893.

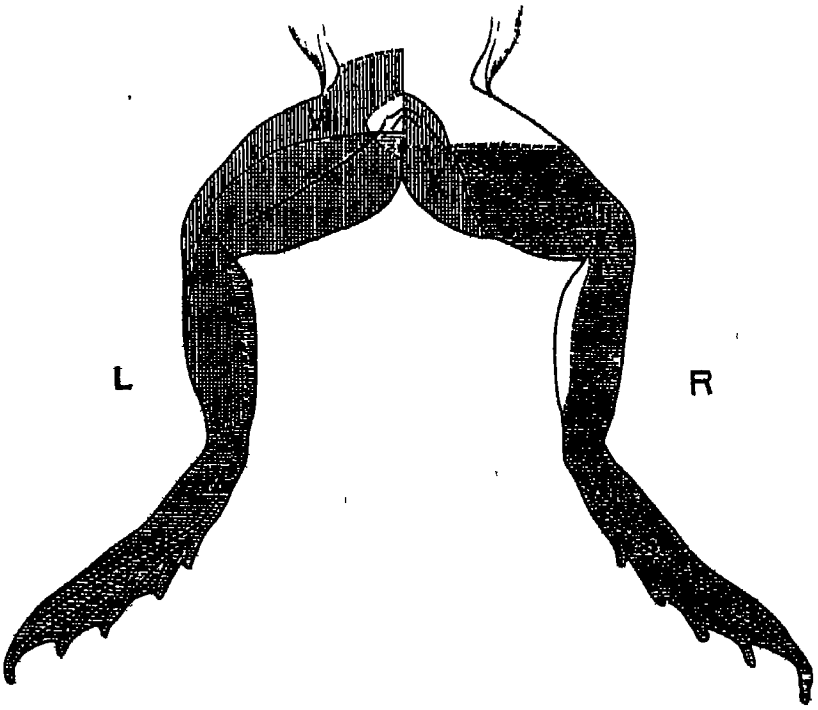
The surface of the hind limb and adjacent part of the trunk was then explored, and the points from which *reflex movements could and could not be initiated* were ascertained. It was assumed that each spot of surface, from which no reflex movement could be elicited, had lost its nervous connection with the spinal cord, and, therefore, did not receive supply from the roots remaining unsevered. The mode of excitation used in the earlier experiments was application of weak induction currents of rapid series. But this plan was soon discarded for stimulation by bits of blotting paper steeped in water acidulated with dilute sulphuric acid. The bits of paper were circles 2 millims across. Mechanical excitation by compression was also employed. During the exploration the Frog was suspended by soft cotton bands under the axillæ, the hind limbs hanging freely. At first my experiments consisted in cutting through a particular nerve-root, and then exploring the limb surface to find a corresponding area of anæsthesia. It soon became clear that the occurrence of muscular movement was more reliable evidence of the existence of afferent ties between the cord and the portion of surface under examination, than was absence of reflex movement an evidence of the non-existence of such ties. In the later experiments, the plan adopted was division of the dorsal nerve-roots immediately above and below the root to be examined; the limits of the area from which a reflex movement could be elicited (*the field of response*), were then determined, and taken as an index of the distribution of the afferent filaments. Each point, whence a reflex movement was initiated, was entered at the time upon a plan of the skin surface previously prepared.

By these methods the field of cutaneous distribution was determined for the dorsal roots of the VIIth, VIIIth, IXth, and Xth spinal nerves respectively, with the following results (figs. 1 and 2):—

VIIth Spinal Nerve.—The anterior border of the cutaneous field passes almost horizontally round one half of the abdomen from a point in the median line of the dorsal aspect to a point somewhat further back in the median line of the ventral aspect. The area embraces the abdomen behind this line, and usually the whole of the thigh, extending also over a tongue-shaped area in the leg that usually nearly reaches the angle. The posterior border of the field passes, therefore, from the middle of the ham over the top of the gastrocnemius to the shin, and reaches the peroneal aspect of the anticus, returning on itself just above the outer malleolus, and following the peroneal edge of the gastrocnemius to the ham. There is also an area around the end of the coccyx and the orifice of the cloaca which is not supplied from the VIIth root. The edge of this area is also part of the posterior limit of the cutaneous field of the VIIth root. The shape and extent of the whole cutaneous field will be gathered better from figs. 1, 2, than from a verbal description. The figures were drawn from the sixth experiment of a series of nineteen made on this root, and are representative of the area as usually existent. There is certainly some variability of the area in individuals. The variation is generally slight, but may be great. When the area was smaller than usual, twice it was found that a strip of the posterior aspect of the thigh along a line roughly corresponding with the course of the sciatic nerve was hardly included, *i.e.*, was continuous with the crural area, whence no reflex could be evoked. On the other hand, in three individuals the whole of the skin of the pes, both dorsal and plantar, especially the former, was supplied by the VIIth root. The risk of error was eliminated by employment of mechanical stimulation; a touch on the dorsum was sufficient to cause flexion of the hip.

VIIIth Spinal Nerve.—The anterior border of the cutaneous field of this nerve runs from near the orifice of the cloaca outward along the back of the thigh, reaching nearly to half way down the front of the thigh, and then sweeping up over POUPART'S ligament to the symphysis, or a millimetre above it. Below that border the whole of the limb, except a longitudinally directed oval area over the calf, is included in the distribution of the nerve. The distribution of the root has been mapped out in ten experiments, and but little variation was detected; once the field of its supply [illegible] crural region, if not entirely, very nearly so. The immediate vicinity of [illegible] end of the coccyx was never included; but the side and ventral edge of [illegible] was part of the ordinary field of the nerve.

Fig. 1.

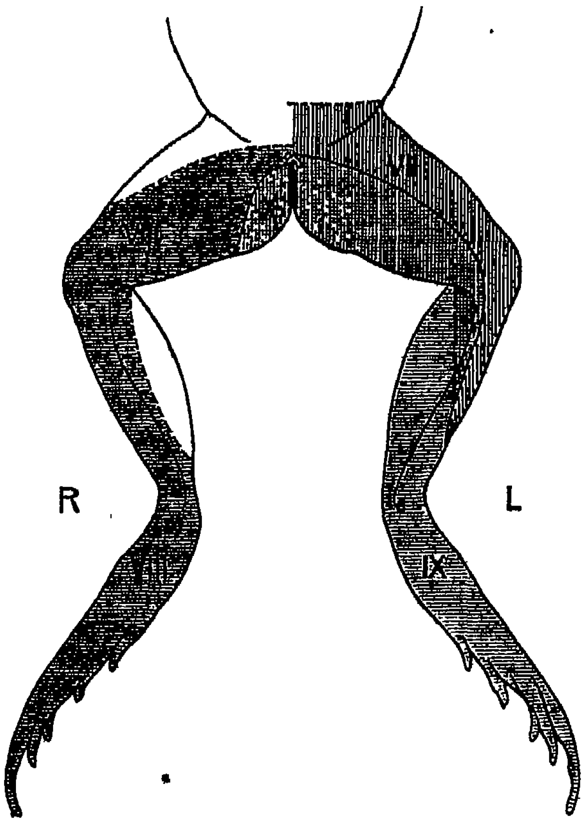


Rana temporaria (dorsal aspect).

IXth Spinal Nerve.—The anterior border of the cutaneous field of the dorsal root of this nerve may be represented by a line starting from the middle line of the back, about midway between the cloaca and the coccyx, and passing outwards and downwards along the posterior aspect of the thigh and knee, to reach the shin about half-way down the leg, and thence be reflected on itself so as to ascend the limb along the inner side of the knee and the ventral aspect of the thigh to the middle line of the hypogastrium at the symphysis pubis, about a couple of millimetres behind the anterior edge of the field of the VIIIth root. The field was delimited in eleven experiments, and no great amount of variation in it detected.

Xth Spinal Nerve.—The cutaneous field of the dorsal root of this nerve is smaller, as is the root itself, than those of the other three nerves examined. It is a tongue-shaped area, the edge of which is represented by a line which starts from the middle line of the back just in front of the coccyx, and passes downward over the hip joint to the back of the thigh, extending about half-way to the ham, and thence returning upward to the middle line of the body below the symphysis pubis. A large portion of this boundary corresponds accurately with the edge of a piece of skin of different character from the skin elsewhere, and beset with glands of a special kind—skin which is modified by sexual character. This field has been delimited in a number of experiments (more than twelve), and has been found to vary considerably, and the size of the patch of sexual skin is also variable. The patch of sexual skin sometimes exceeded the limits of the field of the nerve.

Fig 2.



Rana temporaria (ventral aspect).

The fields of distribution, as thus given, were ascertained at the very outset of the present investigation, and before I had come across the paper by ECKHARD. After reading that, I repeated the delimitation again for each nerve, paying attention to the discrepancies between his description and the above, but found nothing to prevent adherence to the areas, as previously determined and represented in the combined figures given.

The conclusions arrived at by the above examination of *Rana temporaria* proved a basis for the succeeding examination of *Macacus rhesus* and the Cat. I will therefore state them here before proceeding with the description of those other types.

1. Although in a plexus each nerve-root affords contributions to many different nerve-trunks in the plexus, the cutaneous distribution of the root is composed not of patches which are disjoined, but of patches which are so joined that the distribution of the entire root forms one continuous field.

2. The field of skin belonging to each sensory spinal nerve-root overlaps the skin-fields of the neighbouring spinal nerves to a remarkable extent. The disposition of the overlapping is such that the cutaneous field of one sensory root overlaps, to a certain extent, the cutaneous field or fields of the sensory root or roots immediately in front of it, and, to a certain extent, the field or fields of the sensory root or roots immediately behind it. These two overlaps may be termed respectively the *anterior overlap* and the *posterior overlap* of the root-field.

3. The cutaneous field for each posterior root meets the middle line of the body both ventrally and dorsally. Although the transgression of the middle line of the body by the root-field is but slight, yet in most places a slight transgression is unmistakable. A *crossed overlapping* of the cutaneous fields of the right-hand and left-hand posterior roots is thus existent. This *crossed overlap* of the root-fields at the middle line may, on the dorsal aspect, be termed the *dorsal crossed overlap*, on the ventral aspect the *ventral crossed overlap* of the root-field.

4. As judged by its nerve-root supply, the skin at the posterior end of the coccyx is segmentally posterior, even to the skin surrounding the cloacal orifice. Of the skin of the limb, that on the extensor aspect (front) of the thigh is segmentally anterior to the skin of the leg or foot, but that on the flexor aspect (back) of the thigh is of the same segmental level as that of the foot. The most segmentally posterior portion of the skin of the limb is the sexual patch above described.

During the above experiments it was found that in the cutaneous field for each root the peripheral portion of the field was not so irritable as the rest of the field. The edge of the field had no abrupt limit, but the irritability gradually faded at the border zone. Therefore :—

5. In the cutaneous field of each single root the distribution of the particular root is less abundant at and near the edge than elsewhere in the field. The edge of the field is less abrupt at the anterior and posterior overlaps than at the crossed overlaps. It was clear from the experiments that much individual variation exists in the extent of the cutaneous fields of the sensory roots. This was particularly seen with the [illegible]. It is a phenomenon quite similar to that already noted for the [illegible] of these spinal nerves in the Frog by ECKHARD (1),

HALLSTEN[*] and myself[†] and, in the Cat and Monkey by LANGLEY[‡] and myself.[§] In a paper on the arrangement of the motor fibres of the lumbo-sacral plexus, I have, for convenience of reference, treated this individual variation as giving two classes of plexal distribution, a *prefixed* and a *postfixed.* This classification will save periphrasis in the present paper also, and is as applicable to the sensory nerve-roots as to the motor. In an individual with prefixed plexus any particular area of skin is supplied by nerve-roots which lie further headward than those supplying the correspondingly situated skin in an individual with postfixed plexus. For example, in an individual with prefixed plexus, the skin of the dorsum pedis will receive fibres from the VIIth and VIIIth roots; in an individual with postfixed plexus, from the VIIIth and IXth roots only. Not only may the nerve-trunks of the plexus in the former case be called prefixed, in the latter postfixed, but the skin of the dorsum pedis may be also termed prefixed and postfixed, because connected to the spinal cord more anteriorly in the former individual, more posteriorly in the latter. I insist on this because it appears that a plexus which may be prefixed as regards its efferent roots may not be so as regards its afferent, and *vice versâ* (*cf.* my previous paper). Thus, root VII may be distributed to the skin of the foot, the plexus being, then, as regards its afferent fibres, prefixed; root VII may supply not merely thigh muscles but the pretibial, or even the post-tibial muscles, as shown in my previous paper, the plexus being in the latter case prefixed as regards its efferent fibres. On three occasions, having found a root VII distributed to the whole of the skin of the foot, I have examined its distribution to the pre- and post-tibial muscles; twice the root did not supply either of those muscle-groups; so that in two individuals out of the three tested a plexus, with markedly prefixed afferent fibres, was not markedly prefixed in regard to efferent fibres. The skin was "prefixed" in the same limb in which the muscle was not. And I have met one instance in which, although root VII supplied the tibialis anticus muscle, the skin field of that root did not extend lower than usual, *i.e.*, the muscle was prefixed but not the skin. On the other hand, I have seen (*e.g.*, in the third of the three individuals above referred to) an afferent distribution of the prefixed class co-exist with an efferent distribution of the prefixed class, and although the number of my experiments is too small to be a secure guide in the matter, I am led to believe that when the afferent fibres of the plexus are prefixed (or postfixed) usually the efferent are so also. The variation of root attachment to the cord, and the possible independence of the anterior and posterior roots of the same individual in this respect, might perhaps be accounted for by the growing *out* of anterior root into myomere, &c., the growing *in* of posterior root into cord segment. A slight difference of ratio of growth of cord to growth of its circumjacent tissue might involve a measurable variation in the root attachment of different individuals. Such an hypothesis would also explain HERRINGHAM's law that the variation affects a series of roots and not a single root.

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[*] 'Archiv. f. Physiol.,' 1885, p. 167.

[†] *Loc. cit.*, vol. 13, p. 638.

[‡] 'Journal of Physiology,' vol. 12, p. 366.

[§] *Loc. cit.*, pp. 639 and 753.

Although the afferent and efferent divisions of the spinal nerve often exhibit variation independently one of another, no instance was met in which the variation did not appear to apply equally to both right and left sides of the body. In other words, though there is considerable variation in the extent of the skin-fields of the separate roots in different individuals, the pattern of distribution was in every individual bilaterally symmetrical.

The rule enunciated by PEYER (2) that the muscle is innervated by the spinal root which innervates the overlying skin is seen to be sometimes true, but subject to not inconsiderable exceptions. Thus the gastrocnemius muscle supplied by roots VIII and IX, may be covered by skin supplied from VII, VIII, and IX; or the tibialis anticus may be supplied by VII, VIII, IX, and be covered by skin innervated only from VIII and IX.

METHOD OF OBSERVATION EMPLOYED ON CAT.

By exciting in an anæsthetized animal the central end of a nerve trunk containing afferent nerve-fibres, reflex actions of various quality and degree may be initiated. By severance of the afferent rootlets of the spinal nerve or nerves by which a peripheral nerve-trunk is connected with the cord the reflexes originated through it can be diminished or set aside completely; diminished if the peripheral trunk communicate with the cord through the channel of several roots and one but not all of these be severed, set aside completely if the severance include all the lines of the connection. This plan of observation was adopted for the exploration of the spinal connections of the afferent nerve-trunks of the lower limb in the Cat.

Choice of a Reflex.—It is evidently desirable for the purpose to choose as criterion of the existence of afferent nerve-fibres a reflex the quantitative amount of which is at least roughly estimable, a reflex not easily fatigued by repetition, not liable to be occasioned by extraneous occurrences during an experiment nor to be simulated by nervous actions arising intrinsically, and, above all, a reflex capable of being evoked to a clearly detectible extent by excitation even feeble in character. Some trial experiments convinced me that the reflex I had looked forward to as probably the most satisfactory was not so; I had thought that in the arterial blood-pressure, admitting as that does of continuous graphic record, and affected as it is by many afferent channels, a most suitable index could be obtained. However, as my friend Dr. ROSE-BRADFORD early foretold me, it proved unsuitable, and for several reasons. In an afferent limb-nerve excitation sufficient to cause a marked reflex contraction in the musculature of the limb often leaves the blood-pressure trace completely without alteration; the difficulty of maintaining the anæsthesia at so constant a depth that the [illegible] arterial pressure remains the same from half-hour to half-hour is very great; the experiment involves frequently cutting large nerve-roots, and this, with the usually [illegible] severe operation and the prolonged employment of the anæsthetic, combines to induce a tendency to Traube-Hering undulations, destroying the regularity of mean pressure desirable in the detection of transient reflex elevations and depressions. Another reflex sign elicitable is alteration of size of the pupil (SCHIFF,[*] OTT[†]), but under anæsthesia the pupil soon becomes widely dilated and sluggish, and a short trial sufficed to show that as a sign it is neither reliable nor easily legible. Modification of the respiratory rhythm induced by excitation of an afferent limb-nerve was next tested as a guide. It was found more delicate in this respect than either arterial pressure or size of pupil, but it appeared less amenable to excitation of the great sacral roots than to that of the lumbar, especially of the upper lumbar. Indeed, it became evident, when experimenting on respiratory reflexes, that local muscular movement was the least variable and the most obvious evidence of the arrival of impulses in the cord by afferent fibres from the *limbs* and body wall, and that the *occurrence* of the local movement was a more reliable token than was the *absence* of it, considered as a negative.

The locality of the reflex movement varies with the locality of source of the afferent impulses, and the intensity of them. With weak stimulation the movement tends to be confined to the muscles innervated by the same spinal segment irritated,[‡] but it also tends to appear with especial ease in the muscles antagonistic to those, even when of other segments. When the central end of the external saphenous nerve is excited by currents somewhat stronger than, if applied to the posterior tibial trunk, would produce contraction of the gastrocnemius, contraction of the gastrocnemius is evoked, and the contraction of the gastrocnemius may be apparently limited to one head of the muscle if the currents employed be of minimal efficiency. Somewhat stronger excitation produces a reply less locally restricted but still distinctly local in character. These limited reflex movements can be evoked from pure muscular nerves, *e.g.*, the nerve-twigs entering muscles. From the central end of the nerve entering the outer head of the gastrocnemius a contraction of the outer head of the muscle can be obtained which is immediately cut out by severance of certain roots in the spinal canal. So quick appears the reply thus obtained, that it was for some time disregarded, as I thought it but an example of the "paradoxical" contraction. On some occasions it may have been of that nature, but more frequently it ceased directly the posterior roots were severed in the spinal canal. Attention has been called recently to such reflex movements by CHAUVEAU;[§] in the present paper I refer to them merely as constituting the criterion which was employed as best for my purpose, because delicate, readily detectable, and practically unexhausted by the course of experiment.

My experiments were conducted as follows:—The animal was wrapped in cotton wool with the exception of the head and back. The back was shaved and one of the limbs in the region to be examined. The animal was then deeply anæsthetized, and placed on a warm water stage upon the operating table. The spinal cord was then in requisite length exposed in the vertebral canal by removal of a sufficient number of spinous processes and laminæ. The dura mater is usually covered in the lumbar region by a layer of fat, in which there lie embedded largish veins. When this layer is turned back by a blunt "seeker" the cord is seen through the transparent membrane, and the pulsation of the vessels on it is very obvious. A little further preparation suffices to bring into view the nerve-roots at their emergence from the dural sheath. The nerve-root can be divided outside the dural sheath or inside it. The former plan has the advantage of not letting out much of the cerebro-spinal fluid, a condition of prime importance for the prolonged preservation of the normal state of the cord. The latter plan has the advantage of presenting no difficulty to severance of the whole of the afferent root of the spinal nerve without injuring the efferent root, whereas if the severance be made outside the theca, it is, in order to be certain that the whole afferent root is divided, best to sever the entire spinal nerve trunk altogether, and this entails a reduction of the efferent field for motor play by a part. In my experiments, unless otherwise stated, the root was cut inside the theca, and the afferent portion alone was severed. Before carrying out the section of a nerve-root it is important to pass a thread round the root in order to ensure the inclusion of all the root filaments in the section. The large nerve-roots of the lumbo-sacral region are accompanied by veins proportionately large, which may after section give sufficient hæmorrhage to obscure the position of the root; it is therefore necessary to perform the desired section at one closure of the scissors. After the section a pledget of wool with normal saline at 38° C. is laid over the cord, and the soft parts are brought together with accurate adjustment. The peripheral nerve, the root constitution of which is to be examined, is then rapidly exposed at a suitable point through a small incision. Beneath it two threads are carefully laid, the more distal is tied, and the trunk divided just distal to it. The other ligature is drawn tight, and the character of the resulting reflex movement noted. Then one of the nerve-roots already exposed in the vertebral canal is severed, and again the nerve-trunk excited by tying a thread ligature. If, as before, the local movement follow in a clear manner, the test is considered to have given an affirmative, and another root is proceeded with by section. If the local movement is not clearly obtained, the test is repeated with a second ligature applied to a point rather higher up the nerve than was the former one. If a local movement is again not clearly obtained, the trunk is well cleared from tissue with the scissors, and lifted up to sheathed electrodes, and weak induction shock in series of a rate of 100 per second are applied. If this stimulation is followed by no movement even when strong enough to be distinctly unpleasant to the tongue, then it is considered that the afferent connections of the peripheral trunk with the cord had been broken completely through. On the other hand, directly a clear local movement has been observed to follow the excitation, the test is considered to have replied that the nerve has probably still afferent connections with the cord, and another of the spinal roots already exposed is severed. If this severance is immediately followed by inability to re-obtain the movement elicited before, or, indeed, any movement with the strength of stimulus previously employed, it is considered that the previous movement was truly reflex, and that at the last root-section the nerve-trunk under examination lost its last afferent connection with the cord. In each experiment the sections of the posterior roots were made successively in an ascending direction or successively in a descending direction, unless expressly stated otherwise. In most cases in each experiment the corresponding peripheral trunk of the right and left sides was examined at a corresponding point both right and left, and on the right hand the roots were severed in the ascending direction, on the left hand in the descending direction. The result on the right side gave for the individual the upper limit of root connection of the trunk examined, the result on the left side the lower limit for the connection. By observing the difference in the strength of excitation required to elicit the reflex before and after intermediate sections of roots, it was possible to judge roughly the share which the root took in the composition of the peripheral trunk. But the indication so obtained is apt to be fallacious because the degree of anæsthesia influences the amount of reflex obtained.

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[*] "La Pupille consideré comme Esthésiomètre." Paris, 1875.

[†] 'Journal of Physiology,' vol. 2, 443.

[‡] SHERRINGTON, 'Journal of Physiology,' vol. 13, p. 730.

[§] "On the Sensorimotor Nerve-circuit of Muscles." 'Brain,' 1891, p. 145.

Two examples will make clear the above description.

28.3.1890. *Cat.* 4 lb. 6 oz. Ether and chloroform.

Tracheotomy, carotid exposed. The IIIrd, IVth, Vth, VIth, and VIIth lumbar, and the Ist, IInd, and IIIrd sacral, and Ist and IInd caudal nerve-roots exposed and looped in the spinal canal right and left. The IVth dorsal digital nerve and the musculo-cutaneous exposed on the right foot.

11.16. Carotid connected with manometer. Mean pressure 118 millims. Hg. Both vagus nerves divided in the neck.

11.20. Secondary at 15 centims. Current just perceptible to tongue. Excitation of musculo-cutaneous for 30 seconds. Rise of blood-pressure.

11.23. Secondary at 15 centims. Excitation of IVth dorsal digit for 30 seconds. Rise of blood-pressure, not half the increase obtained from musculo-cutaneous.

11.28. Right IInd caudal root cut in the spinal canal.

11.33–37. Excitation of each nerve as before gave results as before.

11.42. Right Ist caudal root cut.

11.46–51. Excitation of each nerve as before.

11.54. Right IIIrd sacral root cut.

11.58–12.2. Excitation of each nerve gave rise as before.

12.5. Right IInd sacral root cut.

12.8–15. Excitation of each nerve gave rise as before.

12.18. Right Ist sacral root cut.

12.23–30. Excitation of each nerve gave rise as before.

12.33. Right VIIth lumbar root cut.

12.36. Excitation of musculo-cutaneous gave rise as before.

12.38. Excitation of IVth digital evoked no alteration in blood-pressure.

12.40. Repeated—no rise obtained.

12.42. Repeated—no rise obtained.

12.45. Right VIth lumbar root cut.

12.50. Excitation of musculo-cutaneous as before gave now no rise of blood-pressure.

12.55. No rise of blood-pressure from musculo-cutaneous.

12.58. Repeated, with same absence of effect.

1.3–12. Left IVth plantar digital and left musculo-cutaneous exposed as on right side.

1.15. Excitation of each gives rise of blood-pressure. The mean blood-pressure is now 97 millims. Hg.

1.18. Left Vth lumbar root cut in spinal canal.

1.20. Excitation of each nerve gives rise on blood-pressure tracing, but the rise is hardly perceptible from the IVth plantar digital.

1.22. Again, with same result.

1.25. Left VIth lumbar root cut in spinal canal. Blood-pressure falls somewhat. Mean pressure at 1.30 is 93 millims. Hg.

1.32. Excitation of musculo-cutaneous nerve gives no obvious indication of blood-pressure trace.

1.35. Traube-Hering undulations have set in. These are not broken by excitation of either musculo-cutaneous or IVth digital nerve. No indication of the excitation is legible on the trace.

1.45. Traube-Hering undulations and somewhat falling blood-pressure. Excitation of IIIrd and IVth digitals (plantar) and of whole musculo-cutaneous above ankle are without effect.

This example illustrates the difficulty constantly presenting itself in the method. The plantar digitals gave way on the left side before their roots had been interfered with at all, and the result from the musculo-cutaneous was vitiated to an indeterminable extent by the same failure.

In contrast with this stands the first experiment, in which a local muscular contraction was used as index instead of an alteration on the blood-pressure trace.

28.4.1890. *Cat.* Small. Ether and chloroform.

Six roots exposed and looped in the spinal canal right and left, and found by *post-mortem* dissection to be the IInd and Ist sacral and the lowest four lumbar. The Ist and IVth plantar digital nerves exposed on right side.

11.43–45. Thread round IVth digital drawn tight gives slight flexion at ankle. Thread round Ist digital drawn tight gives same movement.

11.48. Lowest root on right side (*i.e.*, IInd sacral) divided.

11.52–54. Threads tightened on IVth and Ist digitals give slight flexion at ankle as before.

11.59. Ist sacral root on right side cut. A thread tightened on each nerve gives the flexion as before.

12.5. VIIth lumbar on right side cut.

12.8. Thread tightened on IVth digital gives no movement at ankle or elsewhere.

12.10. Another thread—also without result.

12.12. Thread tightened on Ist digital gives movement at ankle, but feebler than before.

12.15–20. Currents with secondary at 14 centims. applied to IVth digital give no movement, applied to Ist digital give flexion at ankle stronger than with thread at 11.45.

12.23–30. VIth lumbar root on right side cut. Thread tightened on Ist plantar digital evokes no movement anywhere.

12.33. Currents applied as before give no movement.

12.40–50. Ist and IVth plantar digital nerves exposed on left side. When thread is tightened each evokes flexion at ankle.

12.54. VIth lumbar root on left side cut.

12.58–1.9. Thread tightened on Ist plantar digital evokes a dubious movement at ankle. Thread tightened on IVth plantar elicits flexion at ankle, perhaps, weaker than 10 minutes ago. Repeated with threads a centimetre higher up nerve—same effect as before.

1.12. Weak induced currents (perceptible to tongue) evoke a perceptible flexion at ankle from Ist plantar digital; a fairly good flexion at ankle from IVth digital.

1.20. VIIth lumbar root cut.

1 24–35. No movement elicitable through either of the plantar nerves with secondary at 10 centims.

The experiment showed, therefore, clearly that in this individual the Ist plantar digital nerve was connected with the cord mainly by the VIth lumbar root but also by the VIIth root; and that the IVth plantar digital was connected with the cord mainly by the VIIth lumbar root but also by the VIth lumbar root.

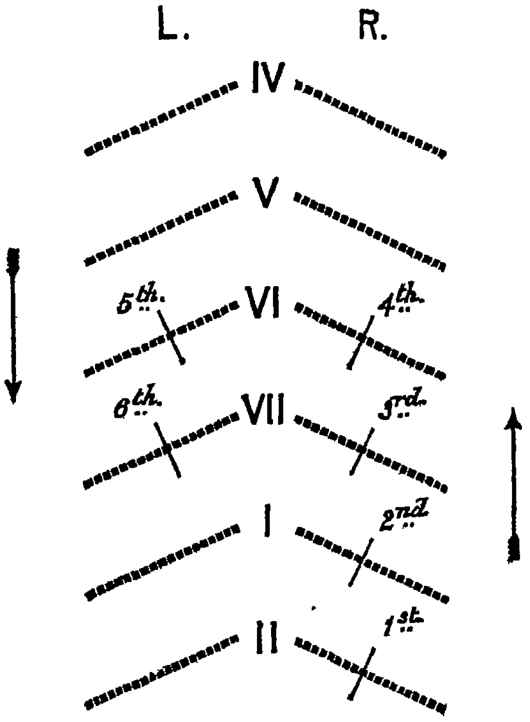
By this method the root-constitution of most of the peripheral nerves of the lower limb was studied; usually in each experiment two small nerves and one large one were taken for analysis.

I will give the experiments in the order in which they were made. From Exp. V. onwards the cord was severed at 6th thoracic segment prior to test of the reflexes.

Experimental Series I. A.

I. *Cat.* Male.

Ist and IVth plantar digital explored, right and left. Movement obtained from each nerve was slight flexion at ankle. 2nd section did not obviously affect either Ist or IVth plantar. 3rd section destroyed IVth plantar, diminished Ist. 4th section destroyed Ist plantar. 5th section diminished Ist plantar very greatly, and IVth plantar dubiously. 6th section destroyed both. Therefore, IVth plantar digital constituted from the VIIth and (?) VIth afferent roots; Ist plantar, from the VIth and VIIth roots.



II. *Cat.* Female.

Ist and IIIrd plantar digitals explored, right and left. Experiment, like I. In Ist plantar digital VIth root > VIIth; but IIIrd digital contains hardly any VIth, almost all VIIth.

III. *Cat.* Female.

Ist and IInd and Vth and VIth collateral digitals (plantar) explored. Sections performed as in I and II.

1st section leaves all nerves unaltered. 2nd section leaves all nerves unaltered. 3rd section reduces reply from Ist and IInd, annuls, or almost so, from Vth digital, and destroys reply from VIth digital. 4th section destroys reply from the remaining digitals under exploration. 5th section (left) reduces the reply from Ist and IInd digitals, and leaves reply from Vth and VIth unaltered. 6th section annuls reply persisting in Vth and VIth digitals.

IV. *Cat.* Female.

IIIrd and IVth and VIIth and VIIIth collateral plantar digitals analysed. Sections as in the previous experiment, except that 1st section was of Ist right sacral; 2nd of VIIth; and 3rd of VIth lumbar; 4th and 5th sections being of VIth and VIIth left lumbar roots respectively.

1st section leaves reply from all the nerves unaltered. 2nd section reduces reply from IIIrd and IVth digitals, destroys the reply from VIIth and VIIIth. 3rd section destroys reply in IIIrd and IVth. 4th section reduces reply from IIIrd and IVth digitals, leaves unaltered the reply from VIIth and VIIIth. 5th section destroys the reply in all.

V. *Cat.* Female.

Ist and IInd plantar collateral digitals, and Ist and IInd and IIIrd dorsal collateral digitals. Sections as in Experiments I–III.

1st section leaves reply from all the nerves unaffected. 2nd section leaves all unaffected. 3rd section leaves reply from IInd plantar less than at first, but the others unaffected. 4th section destroys reply in all, both dorsal and plantar. 5th section destroys reply in Ist dorsal digital, and much reduces reply in all the others, especially IInd dorsal.

VI. *Cat.* Male.

Ist, IInd, IIIrd, IVth, Vth, VIth, VIIth, and VIIIth (α and β) dorsal collaterals. Sections as in Experiment V.

1st section leaves reply from each unaltered. 2nd section leaves reply from each unaltered. 3rd section destroys reply in VIIIth (both α and β divisions of it) and in VIIth, perhaps also the reply from VIth; reduces the reply from Vth and IVth; leaves reply from IIIrd, IInd, and Ist not obviously affected. 4th section destroys reply in all. 5th section (left) destroys reply in Ist and IInd; reduces reply from IIIrd, IVth, and Vth; leaves not obviously altered the reply from the VIth, VIIth, and VIIIth. 6th section destroys reply from all.

VII. *Cat.* Male.

Repetition of last experiment, except that the 1st section was of Ist right sacral, 2nd of VIIth, and 3rd of VIth lumbar; 4th and 5th sections VIth and VIIth left lumbar roots respectively. Results obtained differ a little from those in Experiment VI. The 4th section diminished but did not [illegible] the reply in [illegible] dorsal digital on left side. The 2nd section destroyed the reply in VIth digital, as well as in VIIth and VIIIth of right side.

VIII. *Cat.* Female.

VIth, VIIth, and VIIIth plantar collateral digitals, and VIth, VIIth, and VIIIth dorsal collateral digitals. Sections as in Experiments I–III.

1st section leaves reply from each nerve unaltered. 2nd section leaves reply from each nerve unaltered. 3rd section destroys reply in all nerves, except perhaps slight reply from VIth dorsal digital. 4th section leaves no trace of reply from VIth dorsal digital. 5th section leaves reply from each nerve unaltered. 6th section annuls VIth and VIIth dorsal. Section of 1st sacral annuls all but VIIIth plantar.

IX. *Cat.* Female.

External and internal plantar nerves behind internal malleolus. Sections as in Experiment I.

1st section leaves reply from each nerve unaltered. 2nd section leaves reply from internal plantar unaltered, but reduces reply from external plantar unmistakably. 3rd section reduces reply from internal plantar, and destroys reply external plantar. 4th section destroys reply from internal plantar. 5th section (left) reduces reply from (left) internal plantar, leaves reply from external plantar unaltered. 6th section reduces reply from external plantar, and nearly, but not entirely, extinguishes reply from internal plantar. 7th section (of Ist sacral root) destroys reply from both plantars.

X. *Cat.* Female.

Both plantars and the musculo-cutaneous nerve. Sections as in Experiment I, except that carried one root further downward on left side.

1st section leaves all nerves unaffected. 2nd section reduces perceptibly the reply from external plantar. 3rd section reduces reply from internal plantar and musculo-cutaneous nerve, and extinguishes reply from external plantar. 4th section extinguishes reply from all the nerves. 5th section reduces reply from internal plantar and musculo-cutaneous; reply from external plantar not obviously affected. 6th section extinguishes reply from musculo-cutaneous nerve, not from external plantar or internal plantar. 7th section extinguishes reply from the last, not quite from external plantar.

XI. *Cat.* Female.

Repetition of X, with same results.

XII. *Cat.* Female.

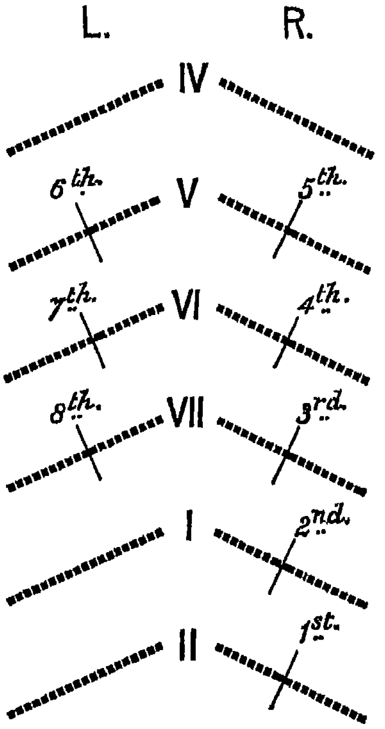
External saphenous nerve on calf, and posterior tibial nerve about 6 centims. above ankle tested. Sections as in Experiment X.

1st section leaves reply from each nerve unaltered. 2nd section leaves reply from posterior tibial nerve not obviously altered, but reduces reply from external saphenous nerve. 3rd section leaves reply from posterior tibial reduced; destroys reply from external saphenous nerve. 4th section extinguishes reply from posterior tibial. 5th section (left) does not obviously affect reply from either nerve. 6th section reduces reply from posterior tibial, much more than reply from external saphenous. 7th section extinguishes the reply from both.

XIII. *Cat.* Female.

Musculo-cutaneous and anterior tibial about 5 centims. below the knee, and the internal saphenous nerve at the knee.

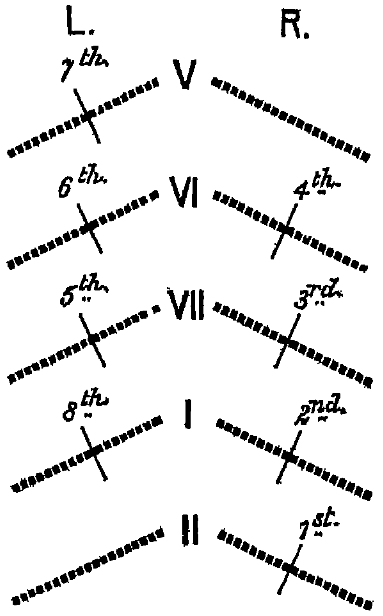
1st section did not alter reply from the nerves. 2nd section did not alter reply from the nerves 3rd section reduced the reply from the musculo-cutaneous and the anterior tibial. 4th section extinguished the reply from the musculo-cutaneous and anterior tibial, and reduced the reply from the internal saphenous nerve. 5th section extinguished the reply from the internal saphenous nerve,



6th section reduced reply from internal saphenous nerve without perceptibly affecting those from the others. 7th section extinguished reply from internal saphenous nerve, and reduced reply from the anterior tibial and musculo-cutaneous. 8th section destroyed the reply from the anterior tibial and the musculo-cutaneous.

XIV. *Cat.* Female.

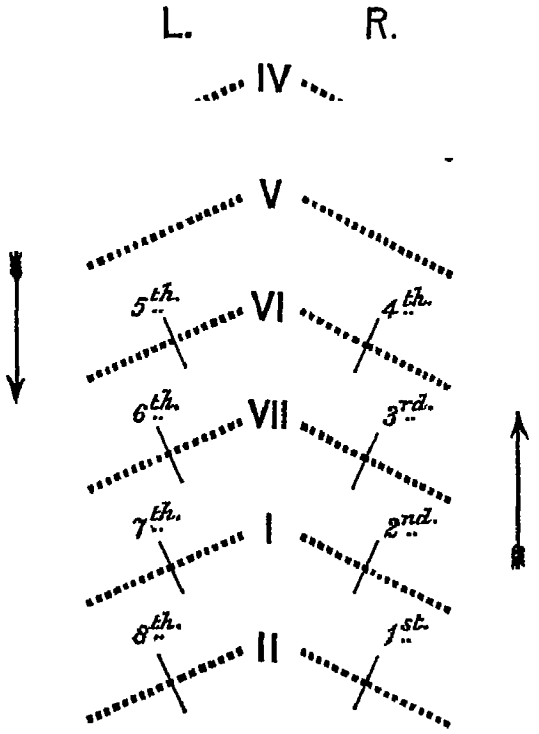
Posterior tibial, external saphenous, and a cutaneous nerve passing from the medial side of the internal popliteal in the thigh to the skin over the outer part of the calf (referred to in note-book for convenience as *x*).



1st section leaves reply from all three unaltered. 2nd section destroys apparently absolutely the reply from *α*, much diminishes reply from external saphenous, questionably reduces reply from posterior tibial. 3rd section destroys reply from external saphenous, reduces reply from posterior tibial. 4th section destroys the reply from the posterior tibial. 5th section (left) much reduces reply from external saphenous nerve, leaves reply from posterior tibial, and from *α* apparently unaltered. 6th section reduces reply from posterior tibial, leaves replies from external saphenous and nerve *α* apparently unaltered. 7th section produces no further alteration. 8th section (*i.e.*, of Ist left sacral) destroys replies from external saphenous and from nerve *α*.

XV. *Cat.* Female.

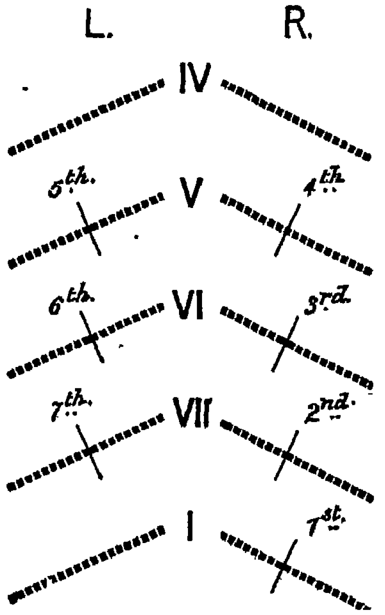
Posterior tibial, external popliteal (behind head of fibula), and a cutaneous nerve arising from the inner side of the sciatic, and passing to skin over the biceps tendon. Sections as in Experiment I, except carried downwards to the IInd sacral on the left side. The cutaneous branch over biceps is designated nerve β.



1st section obviously reduces the reply from nerve β, the rest unaltered. 2nd section destroys reply from β, and obviously reduces reply from posterior tibial. 3rd section obviously reduces reply from external popliteal, and extinguishes the reply from the posterior tibial. 4th section extinguishes reply from external popliteal. 5th section (left) does not obviously affect reply from any of the nerves. 6th section much reduces the reply from the external popliteal and from the posterior tibial; does not affect the reply from nerve β. 7th section extinguishes reply from external popliteal and from posterior tibial, reduces the reply from nerve β. 8th section extinguishes the reply from nerve β.

XVI. *Cat.* Female.

Anterior tibial, musculo-cutaneous, and internal saphenous nerves at the ankle.

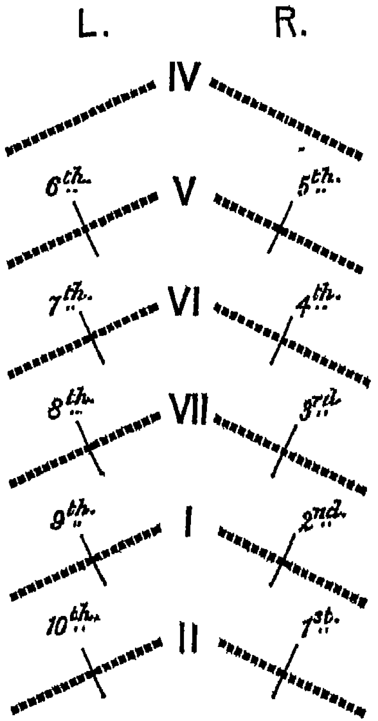


1st section leaves replies from all the nerves unaltered. 2nd section reduces the replies from the musculo-cutaneous and the anterior tibial nerves; does not affect reply from internal saphenous at ankle.

3rd section extinguishes replies from musculo-cutaneous and from anterior tibial, leaves reply from internal saphenous apparently unaltered. 4th section extinguishes reply from all three nerves. 5th section (left) extinguishes reply from internal saphenous nerve at ankle; does not affect replies from anterior tibial and musculo-cutaneous. 6th section diminishes replies from anterior tibial and from musculo-cutaneous. 7th section extinguishes replies from both these nerves. The internal saphenous nerve tested at the top of the thigh gave no reply at the end of this experiment.

XVII. *Cat.* Female.

The internal and external popliteal nerves in the ham, and the internal saphenous in the lower third of the thigh.



1st section does not obviously affect replies from any of the nerves. 2nd section does not obviously affect replies from any of the nerves. 3rd section obviously reduces the reply from each of the popliteal nerves, leaves that from the internal saphenous unaltered. 4th section extinguishes reply from each of the popliteal nerves, and reduces that from the internal saphenous nerve. 5th section extinguishes reply from the internal saphenous nerve. 6th section (left) reduces reply from internal saphenous nerve, leaves replies from the popliteal nerves unaltered. 7th section extinguishes reply from the internal saphenous nerve, does not obviously affect replies from the popliteal nerves. 8th section reduces unmistakably the replies from the popliteal nerves. 9th section extinguishes the reply from the external popliteal, but not that from the internal popliteal. 10th section extinguishes the reply from the internal popliteal. At end of this experiment excitation of central end of the whole sciatic under the gluteus evoked no response, neither did excitation of central end of the obturator on the pectineus muscle.

XVIII. *Cat.* Female.

Internal saphenous nerve at ankle in two branches, an internal (medial) designated *i*, and an external, designated *e*. Anterior tibial on instep in two branches, an inner designated *i′*, an outer designated *e′*. External saphenous nerve about half an inch above the malleolus. Sections as in Experiment XVII.

1st section produces no obvious change. 2nd section causes no alteration in *i* or *e*, nor in *i′* or *e′*, but almost extinguishes external saphenous. 3rd section extinguishes external saphenous, reduces *e′* greatly, *i′* less, does not alter *i* or *e*. 4th section extinguishes *e′* and *i′*, reduces *i* and *e* very greatly. 5th section extinguishes *i* and *e*. 6th section (left) reduces *e* slightly without other change. 7th section extin- [illegible] obviously affecting *i′* or *e′* or external saphenous. 8th section extinguishes *i′* [illegible] external saphenous. 9th section extinguishes external saphenous.

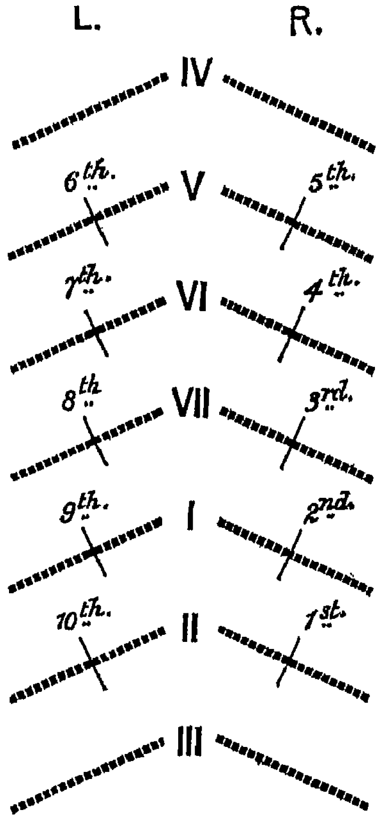
XIX. *Cat.* Female.

Internal saphenous at ankle, then in thigh, rest of anterior crural taken as one trunk in thigh, and obturator on the pectineus muscle. Sections as in Experiment XVI.

1st section produced no obvious change in the reply, which was slight spreading of two innermost toes. 2nd section produced no obvious change. 3rd section almost extinguished the reply from internal saphenous at ankle, but did not quite abolish it. Excitation then applied to the internal saphenous trunk at the lower part of the thigh gave a good reply (slight adduction of thigh). Also good replies of the same character obtained from whole of the anterior crural (except internal saphenous) about 3 centims. below POUPART'S ligament, and from the obturator on the pectineus muscle. 4th section extinguished reply from all three nerves, also from the whole anterior crural including the internal saphenous nerve below the groin, also from the obturator nerve in the pelvis. 5th section (left) reduces the reply from the anterior crural and the internal saphenous in the upper third of the thigh very obviously, and also the reply from the obturator nerve on the pectineus. 6th section extinguishes the reply from all three nerves. At the end of this experiment the crural branch of the genito-crural gave a good reply, which was extinguished by section of the IVth root.

XX. *Cat.* Female.

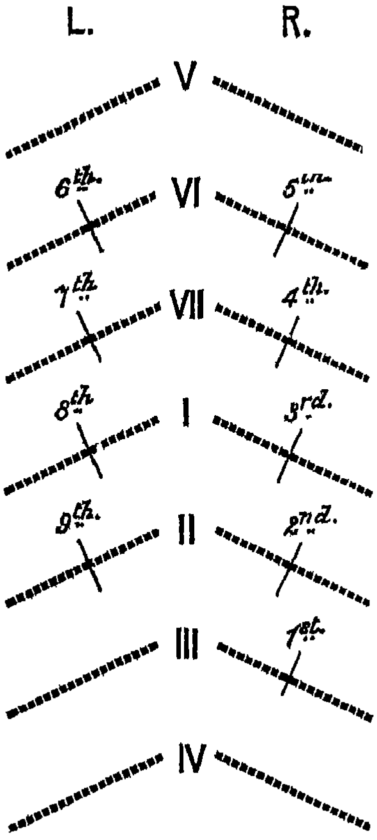
The great sciatic under the gluteus, and the internal saphenous nerve near the knee, in two branches designated *i.s.* and *i.'s.'*; also finally the anterior crural at POUPART'S ligament in one trunk.



1st section produced no obvious alteration in the replies (adduction from the internal saphenous nerve, adduction of thigh, and contraction of the anus from the great sciatic). 2nd section produced no obvious alteration in the replies from the internal saphenous, but diminished that from the sciatic trunk; the reply now is not contraction of the anus, but simply adduction of the thigh. 3rd section produced no obvious alteration in the internal saphenous reply, but extinguished the reply from the sciatic altogether. 4th section greatly reduced supply both from *i.s.* and from *i.'s.'*. 5th section abolished reply from *i.s.* and *i.'s.'*; on excitation of the whole anterior crural at POUPART'S ligament no reply was obtained. (I then excited the distal end of the efferent root of the left IInd sacral, in order to see if it gave fibres to the plantar muscles, and found it did do so.) 6th section just perceptibly diminished the reply from *i.s.* and *i.'s.'*, but did not obviously affect the reply from the sciatic. 7th section nearly abolished the reply from *i.s.* and *i.'s.'*, but not entirely. 8th section extinguished the replies from *i.s.* and *i.'s.'*, and reduced the reply from the sciatic. 9th section reduced nearly to extinction the reply from the sciatic. 10th section abolished it entirely. On *post-mortem* dissection it was found that in this individual the plexus was extremely "post-fixed." No contribution was discovered from root VI to the lumbo-sacral cord. On the other hand, root VII contributed by small branches to the obturator and anterior crural nerves. The experiment shows that the small filaments from root VII to the anterior crural nerve must have contained afferent fibres; it is to be regretted that, in exciting the sciatic as a whole, the opportunity was lost for determining whether these afferent fibres came from the external or the internal popliteal.

XXI. *Cat.* Male.

At the top of the thigh the sciatic nerve consists of three easily separable divisions, the two popliteals and a nerve which may be referred to as the "hamstring nerve," as it supplies the hamstring muscles. The same arrangement holds in *Macacus* also, as I have pointed out in a previous paper. Where the sciatic nerve emerges from the notch two other nerves lie near it, but posterior to it, both of these latter end in skin in the caudo-gluteal region, and may be designated *p* and *p'* respectively. The replies from *p* and *p'* consist in closure of anus and slight abduction and elevation of root of tail. Hamstring nerve evokes flexion of digits.



1st section produced no effect on the replies. 2nd section reduced replies from *p* and *p'* very much. 3rd section abolished replies from *p* and *p'*, and questionably reduced the reply from the hamstring nerve-trunk. 4th section much diminished the reply from the hamstring nerve. 5th section abolished the reply altogether. 6th section (left) did not detectably affect the replies. 7th section much reduced the reply from the hamstring nerve, but did not obviously affect *p* or *p'*. 8th section abolished reply from the hamstring nerve, and certainly diminished that from *p*, not from *p'*. 9th section abolishes reply from *p* and *p'*.

[illegible] above experiments the sections may appear to have been performed on some [illegible] without reason, but it must be remembered that it is not easy to recognize during the experiment the exact identity of an individual root exposed in the spinal canal in the region of the cauda equina. The above experiments were made in uncertainty of the exact segmental numbers of the roots which had been divided. This was ascertained in each case by *post-mortem* dissection, in the following manner. The first rib on each side was exposed and the right and left ribs counted, and the number of the lumbar roots was taken from the last rib. In my notebook no attention was paid to the distinction between lumbar and sacral vertebræ, but all the roots below the last thoracic were termed post-thoracic. In quoting the experiments I have considered that the lumbar roots are seven and the sacral three, in the Cat, because those numbers are in use by Mammalian anatomists. In only one of 22 individuals examined was the number of ribs found to be 12 instead of 13, but in one there were 14 ribs instead of 13. Among the individuals used in the above experiments one had a post-fixed plexus in which root VI gave no discovered contribution to the sciatic trunk, but root VII gave a small branch to the obturator nerve, and a smaller twig to the anterior crural—and this was traced by experiment into the internal saphenous nerve. This degree of post-fixture is not common; I have found and figured it in the Monkey (*cf.* "On the Lumbo-Sacral Plexus," 'Journ. of Phys.'), and I have seen other instances in the Cat. The anterior crural and especially the obturator were found by dissection to receive each a branch from the nerve-root lower than the lowest usually entering them, and in one of these individuals I had found by experiment the gracilis muscle supplied with motor fibres from root VII, the last lumbar, although the lowest root usually supplying the gracilis in the Cat is root VI, the lowest lumbar but one. It is thus clear that individual variation occurs in the building of the peripheral trunks from the sensory roots just as it occurs in the building up from the motor roots. Further, the degree of this variation is often sufficiently great to be revealed by naked eye dissection of the roots of the plexus. When one finds by naked eye dissection a plexus of obviously post-fixed or prefixed type the character of its conformation may be impressed not only on its motor composition but on its sensory, and probably on both together, and in the same sense (*cf.* Experiment XX, and also Experiment of January 19, 1891).

The collective results of the foregoing experiments are arranged in the appended table. A large cross denotes that the root in the same horizontal line of the table had a great share in the constitution of the nerve-trunk. A cross in brackets indicates that the root was sometimes represented in the peripheral nerve and sometimes not. Not all the nerves mentioned were *completely* analysed, *e.g.*, the genito-crural was not.

DISTRIBUTION of Afferent Roots in some Nerves of the Lumbo-Sacral Plexus in the Cat, based on Experimental Series I.

Number of the nerve-root.		Collateral digital nerves.																Int. plantar.	Ext. plantar.	Ant. tibial.	Musc. cutan.	Thigh, Pelvis } obturator.	Thigh, Knee, Ankle } int. saph.	Post-tibial.	Ext. saph.	Int. popl.	Ext. popl.	Hamstring N.	Cutan. br. *α*.	Cutan. br. *p*.	Cutan. br. *p′*.	Gen. crur. (crural).
		Plantar.								Dorsal.																						
		Ist	IInd	IIIrd	IVth	Vth	VIth	VIIth	VIIIth	Ist	IInd	IIIrd	IVth	Vth	VIth	VIIth	VIIIth															
Lumbar	IVth	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+
	Vth	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	++	+++									
	VIth	X	+	+	+	+ (?)	..	..	..	+	X	+	+	+	+ (?)	..	..	+	..	+	+	++	+++	+	..	+	+	+				
	VIIth	+	+	+	+	X	+	+	+	(+)	+	+	+	+	X	+	+	+	+	+	+	..	(+)	+	+	+	+	+				
Sacral	Ist	..	..	+	+	+	+	+	X	..	..	..	..	..	..	..	(+)	(+)	+	..	..	..	..	+	X	+	+	+	+	+	+	
	IInd	..	..	..	..	..	..	..	+ (?)	..	..	..	..	..	..	..	..	..	(+)	..	..	..	..	..	..	+	..	..	..	+	+	
Experiments		I, II, III, V. Exp. p. 18	III, V.	II, IV.	I, IV. Exp. p. 18.	III.	III, VIII.	IV, VIII.	IV, VIII.	V, VI, VII.	V, VI, VII.	V, VI, VII.	VI, VII.	VI, VII.	VI, VII, VIII.	VI, VII, VIII.	VI, VII, VIII.	IX, X, XI.	IX, X, XI.	XIII, XVI, XVIII.	X, XI, XIII, XVI.	XIX.	XIII, XVI, XVII. XVIII, XIX, XX.	XII, XIV, XV.	XII, XIV, XVIII.	XVII, XXI.	XV, XVII, XXI.	XXI.	XV, XX.		XV, XX.	XIX.

X denotes that the root has a predominant share in the nerve-trunk.

(+) denotes that slight but distinct evidence of the root was *sometimes* found.

+ (?) denotes that the evidence obtained was never better than dubious.

A certain number of experiments were made on the Monkey by exactly the same method as those above related in the Cat. The species of Monkey employed was, without exception, *Macacus rhesus*, and, for the most part, immature individuals, *e.g.*, in the females menstruation had hardly commenced. In regard to *Macacus rhesus*, it will be remembered that the lumbar vertebræ are seven as in the Cat, and that the sacral vertebræ are three, but that there are twelve pairs of ribs instead of thirteen as in the Cat. As stated in my paper on the efferent fibres of the lumbo-sacral plexus, the correspondence between the roots of that region in Cat and Monkey, respectively, seems as follows :—

Cat.		*Macacus rhesus.*
IInd lumbar root (? + Ist)	=	Ist lumbar.
IIIrd „	=	IInd „
IVth „	=	IIIrd „
Vth „	=	IVth „
VIth „	=	Vth „
VIIth „	=	VIth „
Ist sacral root	=	VIIth „
IInd „	=	Ist sacral.
IIIrd „	=	IInd „

Further, it must be noted that the foot of *Macacus* has five well developed digits instead of the four of the hind foot of the Cat; I have, therefore, attempted the analysis of twenty instead of sixteen collateral digital nerves.

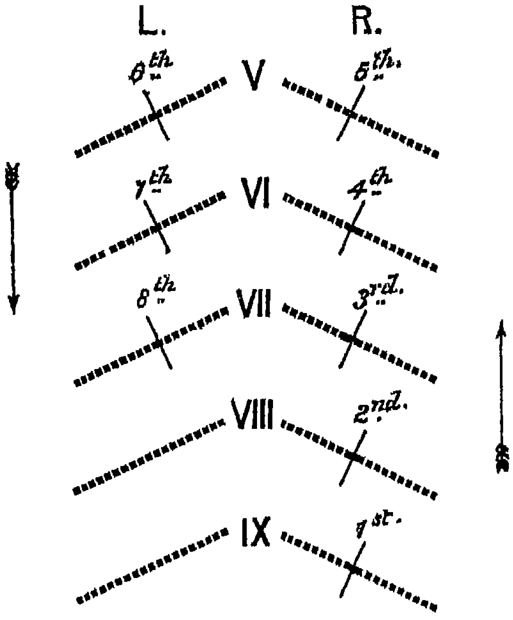
The segmental number of the individual root could only be positively ascertained by *post-mortem* dissection. As with the Cat, the numbering of the roots was always commenced from the first, not from the last rib, and the counting was carried out on both sides.

Experimental Series I. B.

1. *M. rhesus.* Young Female.

Ist, IInd, and IIIrd, and VIIIth, IXth, and Xth dorsal collateral digital nerves analysed for root composition. The reply obtained from each was flexion with adduction of the hallux, occasionally accompanied by slight flexion of other digits as well.

1st section produced no obvious alteration in the reflex replies. 2nd section produced no obvious alteration in the replies. 3rd section cut down the replies from Xth and IXth digitals, the former almost to extinction, but did not affect the other replies at all. 4th section destroyed reply from Xth, IXth, and VIIIth, and reduced replies from IIIrd, IInd, and Ist, the last very slightly; the character of the reply when obtained was now a slight flexion at the ankle. 5th section destroyed the reply in all. 6th section (left) much reduced the reply in the Ist digital obviously, in the IInd slightly, hardly at all in



IIIrd, the three degrees of reduction were a striking series; left the other replies unaffected. 7th section destroyed the replies from I, II, and III, and reduced the replies from the external three, nearly, but not quite abolishing reply from VIIIth. 8th section abolished all reply.

I. *M. rhesus.* Female.

The most internal five collateral dorsal digitals and the VIIIth, IXth, and Xth analysed. Sections as in previous experiment.

3rd section reduced reply from Xth; no other effect. 4th section reduced reply from IIIrd, IVth, and Vth, and abolished reply from Xth, IXth, and VIIIth. 5th section abolished reply from all. 6th section (left) diminished the reply from Ist; no other effect detected. 7th section destroyed reply from the five internal digitals and from the VIIIth; reduced the replies from the other two. 8th section extinguished all the replies.

III. *M. rhesus.* Female.

All the dorsal collateral digits (but the IXth was accidentally injured early in the experiment on the right side). Sections as in previous experiment.

2nd section produced no obvious effect. 3rd section greatly reduced the reply from the Xth, the IXth was in an unsatisfactory condition. The section did not obviously affect any of the other replies. 4th section extinguished the reply in all except the Ist and IInd, and reduced it from both of them. 5th section extinguished all reply. 6th section (left) reduced the reply in the Ist, IInd, IIIrd, and apparently in the IVth, but certainly not in the rest. 7th section extinguished the reply in the Ist, IInd, IIIrd, IVth, Vth, and VIth, and reduced it in the rest, but much less in the Xth and IXth than in the VIth. 8th section abolished all replies.

IV. *M. rhesus.* Female; older than the preceding specimens.

All the plantar digital (collaterals) explored. Sections as in previous experiment.

1st section produced no obvious change in any of the replies. (The replies were in the case of each nerve the same flexion of hallux, with adduction and occasional flexion of 2nd digit seen in Experiments I–III; a slight difference appeared to be, that, in this experiment, contraction and protrusion of the anus occurred with the movement of the hallux sometimes.) 2nd section produced no obvious change in any of the replies. 3rd section appeared to extinguish the reply from the Xth collateral digitals and to diminish the reply from all the others except the Ist. A scale of less and less reduction by the section was most obvious, as the replies were reviewed in series passing from the outer to the [illegible] the sole, although the nerves had taken some time to prepare and must have suffered in isolating from the surrounding adipose tissue. 4th section destroyed the reply from the VIth and VIIth, the VIIIth and IXth, and in the Xth digitals, and diminished it from all the rest, but much more from the Vth than from the Ist. 5th section abolished the reply from all. 6th section (left) greatly reduced but did not abolish reply from the Ist, and reduced the reply from the IInd, IIIrd, and IVth, (?) Vth digital. 7th section abolished replies from the Ist, IInd, and IIIrd digitals, but not from the rest; although appeared to reduce all of them, epecially IVth and Vth, and the Xth and IXth least. 8th section completely abolished replies from all.

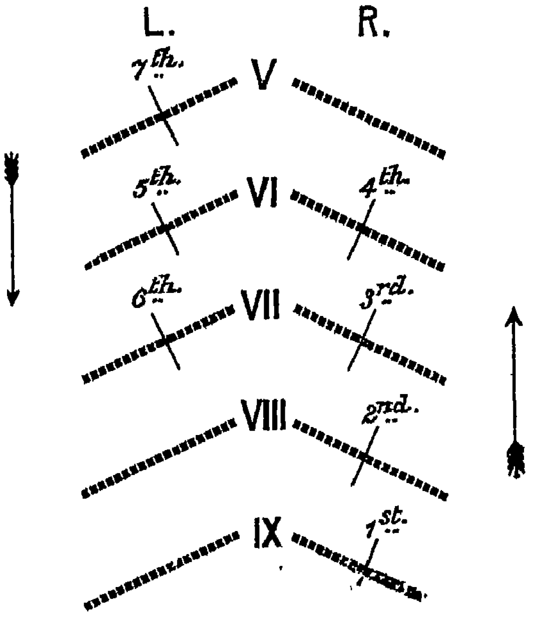
V. *M. rhesus.* Female; young.

The dorsal collateral digitals, I–V inclusive, and the plantar collateral digitals I–V inclusive. The external saphenous about 2 centims. above the external malleolus in two branches, an anterior (*a*), and a posterior (*p*). Sections as in preceding experiment.

1st section did not obviously affect the replies. 2nd section reduced the reply from the external saphenous, *p*. 3rd section reduced the supply from both branches of the external saphenous, and from the Vth, IVth, and (?) IIIrd plantar digitals, but did not obviously affect the reply from any of the dorsal digitals under analysis. 4th section extinguished the reply from the external saphenous, both branches, and from its trunk 2 inches above the external malleolus, and from the Vth, IVth, and IIIrd plantar digitals, and reduced reply from Vth dorsal digital considerably, to less extent from IVth dorsal digital. 5th section extinguished reply from all the digitals, dorsal and plantar. 6th section (left) reduced the reply from all the dorsal digitals under examination except the Vth, and from the Ist and IInd plantar digitals, did not produce any change in the rest, nor in external saphenous. 7th section extinguished reply from all the dorsal digitals, from the Ist and IInd plantar digitals, obviously diminishing it in the other plantar digitals and in the external saphenous, both divisions. 8th section extinguished the reply from the plantar digitals under examination, and nearly extinguished reply from external saphenous *p* but not quite *a*. 9th section was therefore made of the VIIIth post-thoracic root, and this extinguished reply from external saphenous *p*.

VI. *M. rhesus.* Female; young.

The five most external dorsal and plantar collateral digital nerves.



2nd section produced no obvious change in the replies. 3rd section reduced greatly the Xth, IXth, VIIIth, and VIIth plantar, and from the Xth and IXth dorsal digitals, to less extent the reply from the VIIIth dorsal and from the VIth plantar; no other change obvious. 4th section destroyed reply in all the plantar and dorsal digitals examined. 5th section (left) reduced the reply in the VIth, VIIth, and VIIIth dorsal collaterals, also in the VIth plantar. 6th section destroyed the replies from all the dorsal and plantar collaterals under analysis, except the VIth dorsal; this was tested many times over, and appeared to give an indubitable reflex (viz., slight flexion of ankle with some eversion of foot). 7th section was then performed on Vth lumbar root, the movement disappeared at once.

VII. *M. rhesus.* Female; young.

The seven most external plantar collaterals, and the external saphenous nerve above the ankle (about 3 inches above it). Sections performed as in Experiment V.

2nd section produced no obvious change. 3rd section diminished reply from Xth and IXth digitals, and very obviously from external saphenous. 4th section abolished reply from all the digitals under analysis except the Vth and IVth, the reply obtainable from IVth being much better than from Vth (flexion of ankle in each case); reply from external saphenous also completely abolished. 5th section abolished reply from the remaining two digitals. 6th section (left) diminishes reply from none of the nerves examined. 7th section diminishes reply from all the nerves examined; abolishing reply from the IVth digital, or nearly abolishing it. 8th section destroys the reply in all the digital nerves, but not in the external saphenous. 9th section destroys the reply in the external saphenous nerve.

VIII. *M. rhesus.* Female; young.

Five considerable branches of the external cutaneous in the upper half of the thigh, the internal saphenous nerve at the ankle, and the Ist, IInd, IIIrd, IVth, and Vth dorsal collateral digitals analysed. The internal saphenous taken in two twigs. Sections as in Experiment X. The branches of the external cutaneous are taken from without inwards α, β, γ, δ, ϵ.

1st section, 2nd section, and 3rd section produced no obvious change in any of the replies. 4th section extinguished the reply in the Vth and IVth digitals; very nearly extinguished it in the IIIrd digital; reduced it considerably in the IInd digital; and reduced it less in the Ist digital. Did not affect at all the reply from the saphenous twigs, nor from the external cutaneous divisions. 5th section extinguished the reply from each of the two saphenous twigs; certainly diminished somewhat the reply from external cutaneous β, probably from α and γ also; extinguished the reply from each of the digitals under analysis. 6th section greatly reduced reply from each of the divisions of the external cutaneous, but less ϵ and δ than from the others. 7th section abolished reply from all. 8th section affected the reply from five or six branches of the external cutaneous α, β, γ, δ, ϵ, ζ, examined on the opposite thigh to correspond with those examined in right thigh; α and β were affected less than the rest. A nerve found more external and nearer the anterior superior spine was not affected at all, and was found afterwards not to belong to the external cutaneous trunk. 9th section abolished replies from α, β, γ, δ, ϵ, ζ; reduced replies from γ almost to extinction but not quite. Did not affect any of the other replies detectably. 10th section abolished replies from twigs of internal saphenous at ankle; from external cutaneous γ (ζ was not tried because it had become damaged); diminished the replies from the Ist and IInd digitals; but not obviously from the IIIrd. 11th section abolished replies from all the digital nerves under examination. *Post-mortem* dissection showed the plexus in this individual to be of markedly post-fixed type; but I found no branch from root VI to the anterior crural or to the obturator.

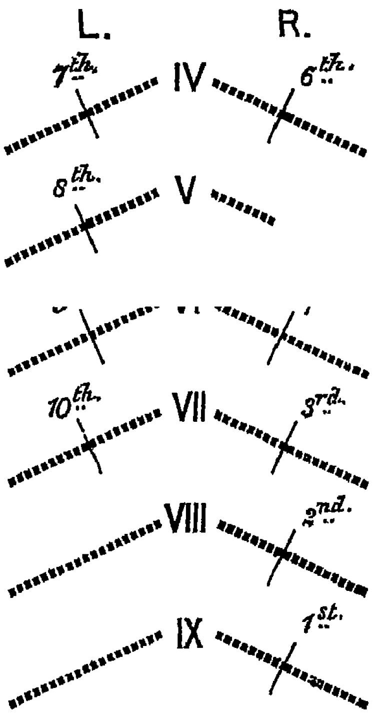
IX. *M. rhesus.* Female; young.

External plantar, internal plantar, posterior tibial, and musculo-cutaneous nerve at ankle. Sections as in Experiment I. The reply consisted in extension at the ankle.

2nd section produced no obvious alteration in reply. 3rd section diminished the reply from the external plantar, and from the musculo-cutaneous. 4th section diminished reply in both plantar nerves, in the posterior tibial, and in the musculo-cutaneous. Before this section was made the anterior tibial at [illegible] been followed into its two divisions, external and internal, and a reply had been obtained from each; the 4th section destroyed the reply from the outer division, but not wholly from the internal. 5th section abolished the reply from all the nerves. The reply from the internal plantar before the 5th section had been very much greater than that from the external plantar, which responded quite feebly. After the 5th section the whole posterior tibial, about 2 inches above the ankle, was tested and gave no sign of reflex. 6th section (left) diminished reply in internal plantar and in musculo-cutaneous nerve. 7th section further diminished replies from internal plantar and from musculo-cutaneous; also from anterior tibial, and from external plantar. 8th section extinguished replies from all, as also from the posterior tibial about 5 centims. above the ankle.

X. *M. rhesus.* Female; older.

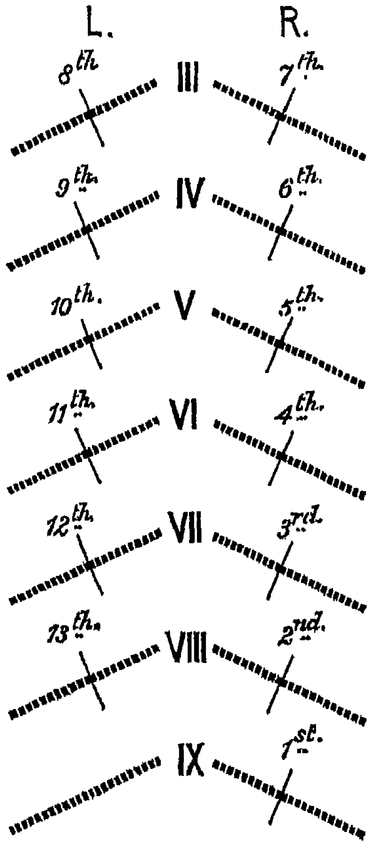
Internal saphenous nerve at ankle, branch from musculo-cutaneous to external plantar branch, the external plantar, the deep branch of the external plantar, cutaneous branch from the sciatic running over the head of the fibula. Sections as in diagram.



2nd section produced no obvious effect. 3rd section reduced almost to extinction the reply from connecting branch between musculo-cutaneous and external plantar; also much reduced reply from deep plantar and from cutaneous branch over head of fibula; did not affect other replies. 4th section extinguished replies from connecting branch between musculo-cutaneous and external plantar, also reply from deep branch of external plantar and from cutaneous branch over head of fibula. Did not apparently affect reply from internal saphenous nerve at ankle. 5th section abolished reply from internal saphenous nerve at ankle. This was tried several times at various intervals; on following the internal saphenous to about 8 centims. above ankle a reply was obtained. 6th section cut out this reply also. The reply from internal saphenous was a movement in the adductor group of the thigh, including in that group the gracilis, but as to whether the gracilis alone, or with other muscles, contracted, I failed to assure myself. On some occasions it seemed the gracilis alone. 7th section (left) did not obviously affect reply from internal saphenous at ankle, nor the other replies (flexion of hallux). 8th section abolished the reply from the internal saphenous nerve at ankle, but did not obviously affect the other replies. 9th section diminished the replies from the deep plantar, and perhaps slightly from the connecting branch, and certainly from the cutaneous passing over the head of the fibula. 10th section abolished reply in the connecting branch, and in cutaneous nerve running by the head of the fibula. The deep plantar nerve was now found to have got damaged, and no further test of it was employed, but the whole external plantar was tested close above the heel, and found to there yield no reply.

XI. *M. rhesus.* Female; young.

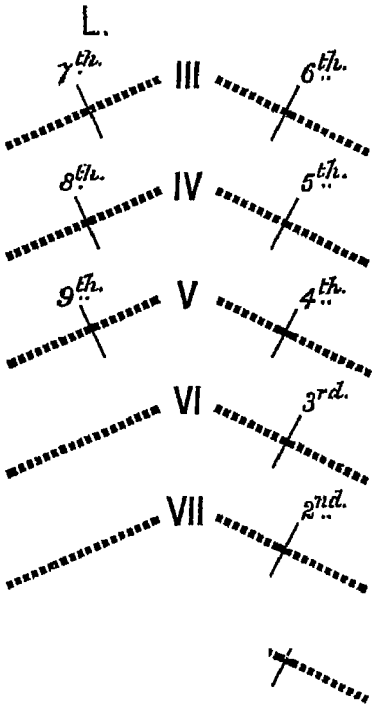
External cutaneous nerve at top of thigh, in divisions, α, β, γ, δ: α the most external, δ the most internal. Internal saphenous nerve at knee, external popliteal and internal popliteal nerves in the ham. Sections as in diagram.



1st section produced no obvious effect. 2nd section produced no obvious effect. 3rd section seemed to diminish reply from internal popliteal. 4th section diminished reply from both popliteals, and (?) from internal saphenous nerve at knee. 5th section decidedly diminished reply from internal saphenous nerve at knee, destroyed reply from internal popliteal certainly, questionably from external popliteal also (both examined in the ham, but not higher). Replies from divisions α, β, γ, δ of the external cutaneous still quite unaffected; these replies consisted in movement at upper and inner part of thigh. 6th section abolished reply in all the nerves except the external cutaneous, and in that diminished the reply about equally in each of its three divisions examined. 7th section abolished replies from each of the divisions of the external cutaneous. 8th section (left) diminished the reply from each of the divisions of the external cutaneous, α, β, γ, δ (these divisions each corresponded, I think exactly, certainly approximately, to the divisions examined on the right side). 9th section abolished the reply from the external cutaneous, α, γ, δ, but not completely in β. It diminished very obviously the reply from the internal saphenous at the knee, but did not affect in a detectable manner the replies from either popliteal. 10th section abolished the reply from external cutaneous, β, and from a small side branch of the internal saphenous close above the knee-joint, but certainly did not abolish completely the reply from the whole trunk at the knee. The reply from each popliteal was still not obviously impaired. 11th section abolished the faint reply from internal saphenous, greatly reduced reply from external popliteal, considerably reduced reply from internal popliteal. 12th section extinguished the reply from the external popliteal in the ham, but left over a fairly good reply from the internal popliteal trunk in the ham. This reply was destroyed by a 13th section through the VIIIth left sub-thoracic root. The reply consisted in contraction of the hamstring muscles, especially those of the outer set. This plexus was found on [illegible] dissection to be remarkably "post-fixed." I did not discover by dissection any branch [illegible] root to the external cutaneous nerve, but if, as not infrequently happens, the external [illegible] sions at a long distance from the vertebral column, and those threads lie imbedded in the psoas, it is possible that such an accession was present and was missed in the dissection.

XII. *M. rhesus.* Male; young; testicles descended.

Internal saphenous nerve about 3 inches below POUPART's ligament; the obturator nerve in two divisions outside the pelvis, the one on the pectineus being α, the deeper β; the internal cutaneous nerve below the knee. Sections performed as in the diagram. The reflex reply from the internal saphenous is in the extensor quadriceps cruris; that from the internal cutaneous also there, but more to the inner side of the muscle; that from the obturator is in the psoas, and the quadriceps extensor about its middle third.

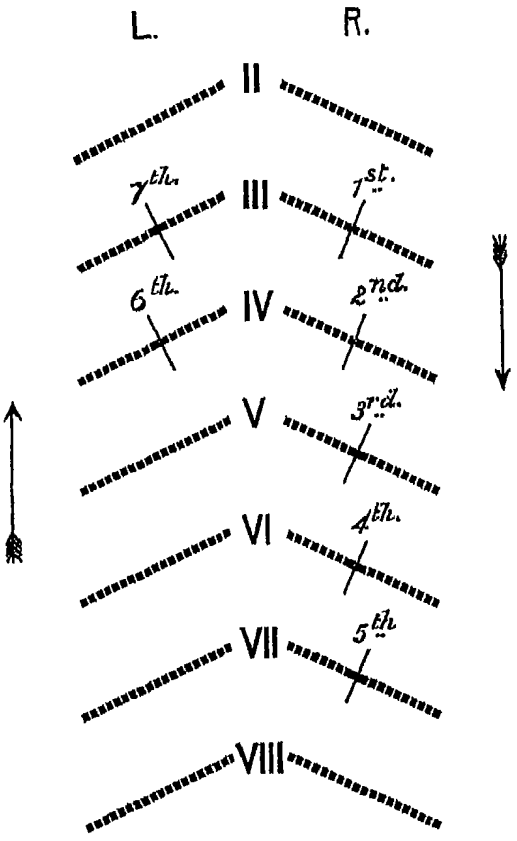


1st section did not change the reply obviously. 2nd section did not obviously affect the reply. 3rd section did not obviously affect the reply. 4th section much diminished the reply from the branch of the internal cutaneous, decidedly also the reply from the obturator β, not obviously the other replies. 5th section diminished the reply from the internal saphenous, destroyed the reply from the internal cutaneous, diminished almost to extinction the reply from the obturator, both α and β. 6th section destroyed the reply from the internal saphenous, and finished the abolition of the replies from the obturator divisions. 7th section (left) diminished the reply from the internal saphenous, but had no obvious effect upon the other replies. 8th section diminished further the reply from the internal saphenous, and diminished obviously the replies from both obturator divisions and from the internal cutaneous branch below the knee. 9th section abolished all the replies. The crural twig of the genital crural gave a slight reflex retraction of the testicle at the end of this experiment.

XIII. *M. rhesus.* Male.

External cutaneous (two branches of) at the upper part of the thigh; the anterior tibial nerve in two branches near its origin from the peroneal; the musculo-cutaneous low down above the ankle; the obturator as three branches in the thigh. Sections performed as in diagram.

1st section diminishes the reply from the external cutaneous, both branches; does not affect the other replies. 2nd section abolishes the reply from the outer of the two branches of the external cutaneous, but not completely from the inner. 3rd section abolishes the replies from all three branches of the obturator, does not affect the other replies at all. 4th section greatly reduces the reply from the ante-



rior tibial nerve, and obviously diminishes reply from the musculo-cutaneous. 5th section abolishes the reply from the anterior tibial and from the musculo-cutaneous, but the reply from the external cutaneous still remains distinct (from the inner branch of the pair tested). 6th section (right, IVth lumbar) reduces reply from obturator obviously. 7th section nearly destroys the reply from the external cutaneous (right side), but not completely.

XIV. *M. rhesus.* Female; young.

Internal cutaneous nerve in thigh examined in four divisions—α, β, γ, δ. Branch of internal saphenous given off from trunk about 5 centims. above the knee. The whole obturator nerve just outside the pelvis. ? The middle cutaneous branch of the anterior crural. Of the divisions of the internal cutaneous, the most external is α, the most internal δ. Sections performed just as in the last experiment.

1st section, no effect. 2nd section, no change detected. 3rd section, no effect detected. 4th section diminished the reply from the internal cutaneous branches, especially β, γ, and δ, from the branch of the middle cutaneous, but to less extent. Considerable diminution in the reply from the obturator nerve. No obvious diminution in the side branch from the internal saphenous nerve, nor perhaps in the middle cutaneous nerve. 5th section abolished the replies from all the divisions of the internal cutaneous, not quite from the middle cutaneous, but quite from the side branch of the internal saphenous, and completely from the whole obturator trunk. It was well seen in this experiment that the 4th section reduced the reply from the obturator more than did the 5th section. 6th section abolished the reply from the ? middle cutaneous. 7th section (left) produced no obvious effect on the trunks under analysis. 8th section abolished reply from a side branch of the internal saphenous above the knee, and greatly reduced the reply from all the branches of the internal cutaneous, α, β, γ, δ. (I am not sure that these accurately corresponded with those taken on the right side, but γ probably did quite accurately.) A questionable reduction in the amount of reply from the obturator trunk. No middle cutaneous found. Of the divisions of the internal cutaneous, it was not clear that α, the most external, did not suffer by [illegible] section almost abolished reply from it. 9th section abolished the replies from [illegible] from the obturator trunk, from which a distinct reply was still elicit[illegible] reply. On *post-mortem* dissection, the plexus was found markedly post[illegible] individual of Experiment X.

XV. *M. rhesus.* Female; young.

The hamstring nerve in two divisions α (outer), β (inner); the crural branch and the genital branch of the genito-crural; the internal cutaneous, in three divisions, close below POUPART's ligament. Sections as in Experiment XI.

1st section, no obvious change in the replies. 2nd section, no obvious change in the replies, except a diminution in the reply from each division of the hamstring nerve. The reply from each division of the hamstring nerve is a slight flexion of ankle, and flexion of hallux. 3rd section, the reply from the hamstring nerve is abolished in both parts; the replies from the other trunks not obviously altered. 4th section, the reply from the genito-crural divisions is not obviously altered; that from internal cutaneous is lowered in all three divisions. 5th section, the reply from the genito-crural divisions is unaltered; that from internal cutaneous is destroyed in each division. 6th section, the reply from the crural branch of the genito-crural, contraction of psoas is diminished but not abolished; the reply from the genital branch seems to be abolished. 7th section (left), the reply from the crural branch of the genito-crural is nearly, but not quite, abolished. 8th section, the reply from the internal cutaneous is much diminished, except in the middle of the three divisions. 9th section, the reply from the internal cutaneous is abolished. 10th section (of the VIth lumbar root), the replies from the two divisions of the hamstring nerve which were isolated are now diminished, but had not been so by the earlier section. 11th section (of the VIIth lumbar root) seems to extinguish the replies from the hamstring divisions, both of α and β, altogether.

XVI. *M. rhesus.* Female; young.

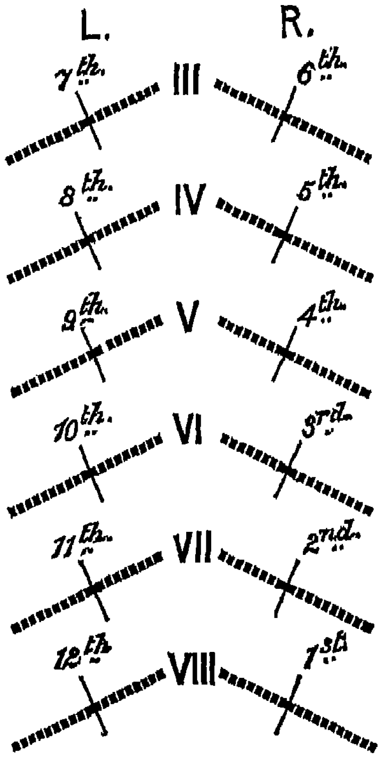
Two long cutaneous nerves passing over the back of the fibula; the branch of the hamstring nerve to the inner hamstrings, and two to the outer hamstrings. The internal and external popliteal nerves below the gluteal region. Sections performed as in Experiment I.

2nd section produced no obvious change. 3rd section diminished replies from all the nerves, especially from the three branches of the hamstring nerve. 4th section abolished replies from the branches of the hamstring nerve, from the cutaneous fibular branches, and almost from the internal popliteal, though not from the external popliteal. 5th section abolished all the replies. 6th section (left) produced no obvious change. 7th section diminished very greatly the replies from the two cutaneous fibular branches, and diminished the replies from the branches, external and internal, of the hamstring division of the sciatic nerve, also detectably from the external popliteal. 8th section abolished all replies from the two cutaneous nerves, also apparently from the hamstring nerve, also from the external popliteal trunk, but not from the internal popliteal. 9th section abolished reply from the internal popliteal trunk (9th section was of VIIIth left-hand sub-thoracic root).

XVII. *M. rhesus.* Female; young.

Branch toward skin passing head of fibula, the external saphenous below the ham not far from its origin, the internal saphenous just above the internal malleolus. A cutaneous branch from the anterior crural, apparently corresponding with the middle cutaneous of Man, taken in four small branches, α, β, γ, δ, in the upper part of the thigh.

1st section certainly diminished reply from external saphenous. 2nd section abolished reply from external saphenous, weakened that from cutaneous branch near the biceps tendon, did not affect the other replies. 3rd section abolished reply from the nerve near the biceps, did not affect replies from branch of anterior crural, nor from internal saphenous. 4th section did not abolish reply from internal saphenous near the ankle, but reduced it very greatly; reduced very much reply from middle cutaneous in all its four branches. 5th section abolished reply from internal saphenous, and from all of ? middle



cutaneous except branch β (the most internal one). 6th section abolished that reply also—a slight contraction in the region of the pectineus and adductor longus. 7th section (left) produced no obvious effect on the replies from any of nerves (the branches of the ? middle cutaneous examined on this side were three in number and certainly did not exactly correspond with those used on the right side). 8th section diminished distinctly the reply from each of the three branches of the middle cutaneous, but not that from internal saphenous at internal malleolus. 9th section abolished the replies from the ? middle cutaneous (each of its branches) and from the internal saphenous; no effect on other replies. 10th section reduced reply from nerve near biceps, but reply from external saphenous remained unaltered. 11th section much reduced reply from external saphenous, and abolished reply from nerve near biceps tendon. 12th section abolished all reply. The condition of the animal was not good, the extremities having become very cold, but a subcutaneous nerve twig near the anterior superior spine gave a good reply, as in Experiment VIII, so that in each case the nerve must have been connected with a root above the IIIrd lumbar.

The collective results of the foregoing series of experiments are for the sake of clearness of comparison placed in a tabular form, as were the results obtained on the Cat. Each large cross denotes that the spinal root it lies opposite contributed largely to the nerve. Crosses in brackets mean that the root did not appear to contribute to the nerve-trunk in all individuals, but did in some.

DISTRIBUTION of the Fibres of the Afferent Roots in some Nerve-trunks of the Lumbo-sacral Plexus of *Macacus rhesus*, based on Experimental Series I. B.

Number of the nerve-root.		Collateral digital nerves. Dorsal. Ist	IInd	IIIrd	IVth	Vth	VIth	VIIth	VIIIth	IXth	Xth
Lumbar	IIIrd	...	...	...	...	...	...	...	...	...	...
	IVth	...	...	...	...	...	...	...	...	...	...
	Vth	X	X	X	X	+	+	...	...	...	...
	VIth	+	+	X	X	X	X	X	X	+	+
	VIIth	...	...	...	...	...	...	(+)	+	+	+
Sacral	Ist	...	...	...	...	...	...	...	...	...	...
	IInd										
Experiments.		I, II, III, V, VIII.	I, II, III, V, VIII.	I, II, III, V, VIII.	II, III, V, VIII.	II, III, V, VIII.	III, VI.	III, VI.	I, II, III, VI.	I, II, VI.	I, II, III, VI.

Number of the nerve-root.		Collateral digital nerves. Plantar. Ist	IInd	IIIrd	IVth	Vth	VIth	VIIth	VIIIth	IXth	Xth
Lumbar	IIIrd		...	...	...	...	...	...	...	...	...
	IVth	...	...	...	...	...	...	...	...	...	...
	Vth	X	X	+	+	+	...	...	...	...	...
	VIth	X	X	X	X	X	X	+	+	+	+
	VIIth	...	(+)	+	+	X	X	X	X	X	X
Sacral	Ist	...	...	...	...	...	...	...	...	...	...
	IInd										
Experiments.		IV, V.	IV, V.	IV, V.	IV, V, VII.	IV, V, VII.	IV, VI, VII.	IV, VI, VII.	IV, VI, VII.	IV, VI, VII.	IV, VI, VII.

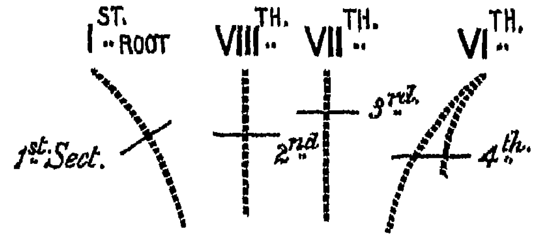
Number of the nerve-root.		Int. plantar.	Ext. plantar.	Anter. tibial.	Musc. cutan.	Thigh obturator.	Pelvis obturator.	Thigh int. saph.	Knee int. saph.	Ankle int. saph.	Post. tib.
Lumbar	IIIrd	...	...	...	...	(+)	(+)	+			...
	IVth	...	...	...	...	+	+	X	X	(+)	...
	Vth	+	(+?)	+	+	+	+	+	+	+	+
	VIth	+	+	+	+	(+)	(+)	...			+
	VIIth	+	+	...	+	...		...			+
Sacral	Ist	...	...	...	...	...		...			+
	IInd										
Experiments.		IX.	IX, X.	XIII.	IX, XIII.	XII, XIII, XIV.		VIII, X, XII, XVII.			IX.

Number of the nerve-root.		Ext. saph.	Int. popl.	Ext. popl.	Hamstring N.	Ext. plantar (deep).	Ext. br. of ant. tib. N. on the ankle.	Cutan. br. from ext. popl. over head of fibula.	Br. from ext. saph. to ext. plantar.	Above patella ext. cutaneous.	Below patella ext. cutaneous.	Crural genito-crural.	Genital genito-crural.	Above knee int. cutaneous.	Below knee int. cutaneous.
Lumbar	IIIrd	...	...	...	...	...	...	...	...	+		+	+		
	IVth	...	...	...	...	...	...	...	...	+	+	...		X	+
	Vth	...	+	+	...	...	...	...	...	...		...		+	X
	VIth	+	+	+	...	+	+	+							
	VIIth	+	+	+	+	...	...	+	+						
Sacral	Ist	+	+												
	IInd														
Experiments.		V, VII, XVII.	XI, XVI.	XI, XVI.	XV, XVI.	X.	XIII.	X, XVI, XVII.	X.	VIII, XI, XIII.		XV.		XII, XIV, XV.	

For the sake of comparison with the arrangement found in the hind limb, a certain number of experiments were made upon the nerves of the fore limb in the Cat by the same method as that employed upon the hind-limb, with one difference. I was not aware at the time with what little risk of hæmorrhage section of the posterior roots of the brachial spinal nerves can be performed inside the vertebral canal. I therefore, instead of performing the sections in the vertebral canal as had been done in the experiments on the pelvic limb, divided in the case of the brachial nerves, the entire nerves outside the vertebral canal, as did PEYER, KRAUSE, and TÜRCK in their experiments. The sources of fallacy attaching to this method I have already mentioned, but the results are given here because so completely harmonizing with the results on the lower limb. The operation presents no difficulty, the chief point being that the upper surface of the 1st rib must be carefully exposed to view in a good light.

Experimental Series I. C.

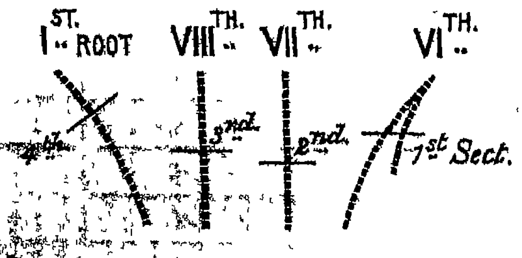
Experiment I. *Cat.* Female. 27.6.1890.



Six digital nerves examined on the dorsum of the right fore foot. Also later, the ulnar trunk and the radial trunk, each 3 centims. above the wrist. Later the posterior interosseous trunk near its origin.

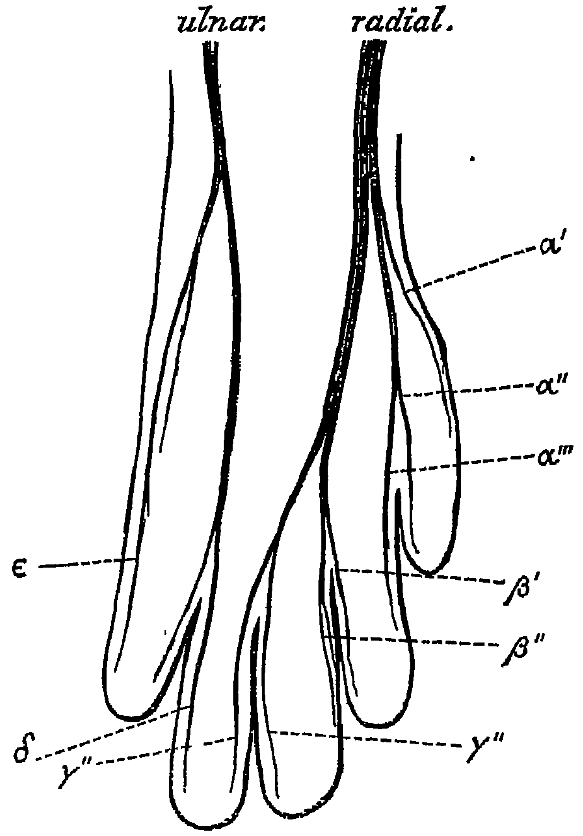
1st section, reply remains in all the dorsal digitals. 2nd section, destroyed reply from the VIth and VIIth dorsal digitals, both from the ulnar trunk. Also destroyed reply in ulnar trunk above wrist. 3rd section destroyed reply from all the digitals under examination; also from the radial trunk above the wrist, but not from a cutaneous branch near, which was afterwards traced up to lie beside the musculo-spinal trunk about the elbow, but not traced further. Also 3rd section destroyed reply from the posterior interosseous. 4th section destroyed reply from the cutaneous nerve above-mentioned.

Experiment II. *Cat.* Female. 30.6.1890.



[illegible]

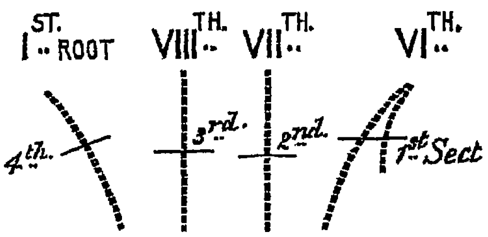
[illegible] analysed under nomenclature in figure.



Dorsum of fore-foot.

1st section, no effect upon any of the replies detected. 2nd section, abolished replies from α', α'' α''' lessened obviously from β'. 3rd section, abolished the replies from β' and β''; diminished replies from γ'. 4th section, abolished the replies from all the remaining digitals under examination.

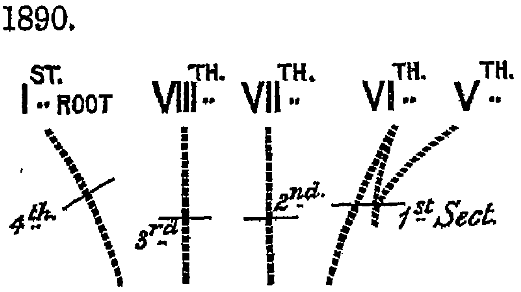
Experiment III.—*Cat.* Female. 1.7.1890.



Analysis of dorsum of hand and forearm.

1st section abolished reply from a large cutaneous nerve passing down the radial edge of the forearm and derived from below the biceps close above bend of elbow, but left reply from the seven dorsal digitals under analysis unaltered. 2nd section abolished reply from the three outermost dorsal collaterals of the radial trunk. 3rd section reduced the reply from the two outermost of the ulnar dorsal collaterals considerably. 4th section abolished reply from all the digital nerves under examination. A smart reply was obtained from the posterior interosseous near its origin until the 3rd section was made.

Experiment.—*Cat.* Male. 2.7.1890.

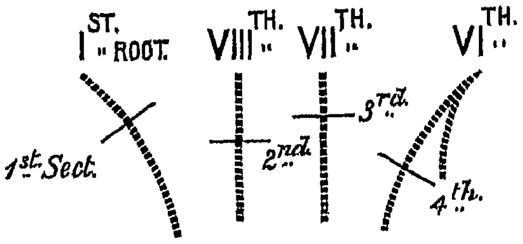


Analysis of nerves of palm.

Ist plantar collateral = α, IIIrd ditto = β, IVth ditto = γ, Vth ditto = δ, VIth ditto = η, VIIth ditto = ζ, VIIIth ditto = ϵ, IXth ditto = θ, Xth ditto = κ, IIIrd dorsal collateral = β'.

1st section abolished reply from none, nor obviously diminished reply, except from α, β, β'. 2nd section abolished reply from α, β, β', γ, δ, and greatly reduced the reply from η, and obviously reduced it from ζ. 3rd section abolished reply from the remaining digitals under analysis.

Experiment IV.—*Cat.* Female. 3.7.1890.

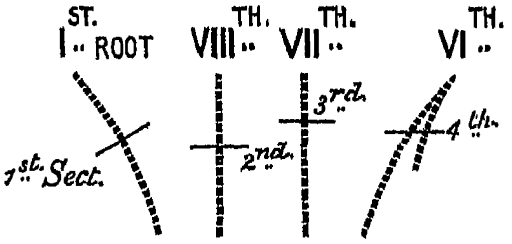


Nerves of the right palm.

The IIIrd palmar collateral = α, IVth ditto = β, Vth ditto = γ, VIth ditto = δ, VIIth ditto = η VIIIth ditto = ζ, Xth ditto = ϵ.

1st section reduced the reply obviously from ϵ, not obviously from ζ. 2nd section abolished reply ϵ and ζ, reduced it greatly from η. 3rd section abolished reply from all the digital nerves under examination. The trunk of the radial, 3 centims. above the wrist, was now examined in two natural divisions, a larger, κ, and a smaller, λ, containing the nerves to the pollex and anterior side of index. No reply was obtainable from κ, a good reply from λ, and also from a twig of the external cutaneous nerve near. Section of the part of the VIth root shown in diagram abolished replies from λ and from external cutaneous at point examined.

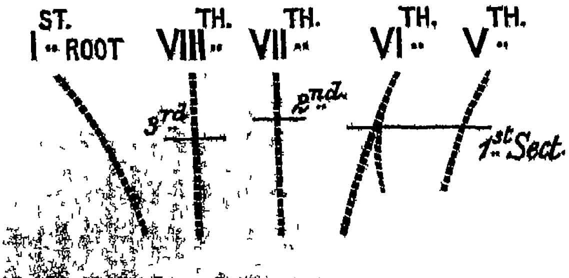
Experiment V.—*Cat.* Female, young. 5.7.1890.



The branches of the musculo-spiral trunk examined.

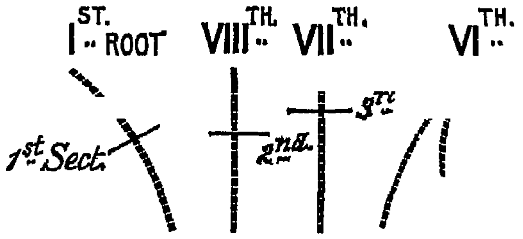
Above the elbow the posterior interosseous and the radial divisions of the musculo-spiral were easily distinguished. Five branches of the former were followed down, two branches of the latter, also a branch from the main trunk toward the external part of the triceps, and a second to the supinator longus. 1st section no effect. 2nd section appeared to reduce reply from two of the branches of the posterior interosseous division. 3rd section abolished reply from nerve toward outer part of triceps nerve to supinator longus, and from the posterior interosseous division of the nerve as a whole. Reply from radial division still obtainable though diminished. The Ist and IIIrd dorsal collateral digitals examined at this stage gave replies obviously weaker from the IIIrd than the Ist.

Experiment VI.—*Cat.* 10.7.1890.



[illegible] the musculo-spiral and the posterior interosseous gave no clear reply after the [illegible]

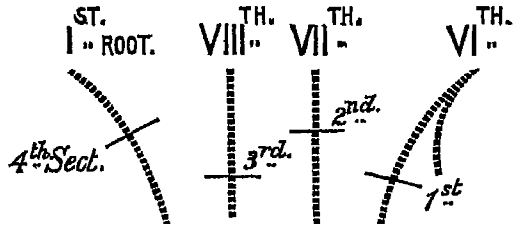
Experiment VII.—*Cat.* 12.7.1890.



Branches of the median and ulnar examined.

1st section abolished reply from none of the nerves examined. 2nd section abolished reply from the anterior interosseous (two side branches, and then the whole trunk tested), from the deep ulnar in the palm, from a branch from the ulnar trunk to the skin over the lower end of the ulna; from all the dorsal and palmar ulnar digitals, and ? from the communicating branch with the median. The replies from the median digitals were damaged toward the ulnar side—but none destroyed. The 3rd section abolished the replies from them also.

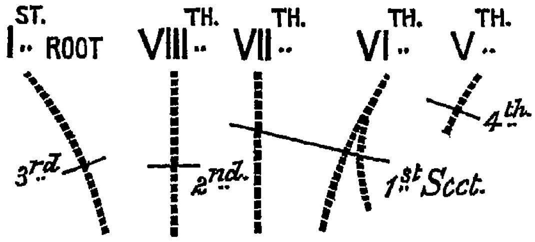
Experiment VIII.—*Cat.* 14.7.1890.



Branches of median and ulnar trunks examined.

1st section seemed to reduce the reply from the Ist palmar collateral digital (median). No other effect detected. 2nd section reduced reply from IIIrd and IVth collateral palmar digitals obviously. 3rd section abolished reply from IIIrd, and IVth, and Vth palmar collaterals, reduced it greatly from VIth, and less from VIIth. Communicating branch between ulnar and median still replies; very brisk replies from the VIIIth, IXth, and Xth palmar collaterals. A reply was obtainable from a branch of the median given off close above wrist, and passing to skin; a reply was also obtainable from muscular branches of the median near the elbow. 4th section destroyed these replies, and also reply from ulnar trunk half way up to elbow.

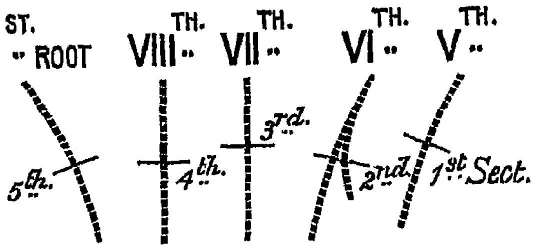
Experiment IX.—*M. rhesus.* Female. 2.9.1890.



Branches on back of hand and forearm examined.

1st section appeared to reduce, but did not abolish reply from the two most radial dorsal collaterals; it appeared to abolish reply from the musculo-cutaneous in the skin near the wrist. 2nd section abolished reply from the four most radial digital nerves, and obviously reduced it in Vth and VIth, 3rd section extinguished reply from all the ulnar digitals and from the ulnar trunk as high as 2 centims. above the wrist, where a fine twig joined it. From these upward it gave a good reply. A branch of the musculo-spiral to skin over triceps also gave a reply. These replies were not abolished by section of the Vth cervical trunk.

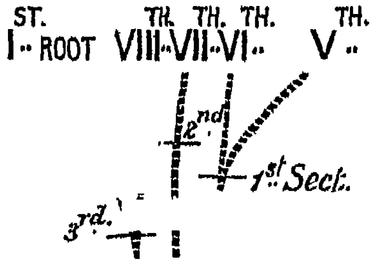
Experiment X.—*M. rhesus.* Female. 3.9.1890.



Nerves of hand and forearm, &c. Left arm.

1st section, no effect obvious on any of the digital nerves nor on branches of the musculo-cutaneous close above the wrist. 2nd section, no effect obvious on any of the digital nerves. The reply from one large branch of the musculo-cutaneous in the forearm is abolished, but not the reply from the other. 3rd section, replies from musculo-cutaneous in forearm abolished; from Ist and IInd palmar and dorsal digitales collaterales reduced. 4th section, replies from Ist, IInd, and IIIrd collateral digitals, both dorsal and plantar, abolished; from the IVth, Vth, and VIth dorsal collaterals obviously diminished; from the IVth palmar collateral obviously diminished. 5th section, replies from all the digitals abolished, also from the internal cutaneous at the elbow. But the skin over and to an inch below the inner condyle and also the skin behind the outer condyle, continued to give replies after the 5th section.

Experiment XI.—*M. rhesus.* Female. Not very young. 4.9.1890.

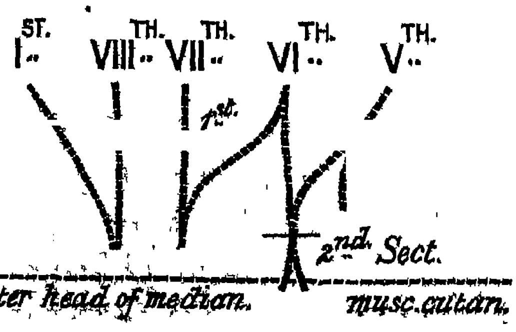


The back of the hand.

1st section reduced greatly the reply from twigs of the musculo-cutaneous along the radial edge of the forearm. Did not obviously affect any of the dorsal digital nerves. 2nd section reduced considerably the replies from the Ist and IInd dorsal collateral digitals, but did not obviously affect the rest. 3rd section abolished the replies from all the digitals, also from the ulnar, internal cutaneous, and median trunks in the axilla; also from the musculo-spiral 3 centims. above the elbow. In this experiment a striking example of local "shock" occurred; after the 2nd section no reply at all was obtainable from the Ist and IInd dorsal collaterals for 20 minutes, although later replies were easily obtained.

After the 3rd section replies were obtainable from a long region down the back of the arm to well below the elbow, and also from the front and top of the shoulder. For limits, see sketches.

Experiment XII.—*M. rhesus.* Female. 5.9.1890.



[illegible] nerves and others.

[illegible] did not obviously affect any of the digital nerves, either plantar or dorsal, at all, nor two large branches of the internal cutaneous examined half way up the upper arm. 2nd section did not obviously affect any of the digital nerves, either plantar or dorsal; the twigs of the musculo-cutaneous on the front of the forearm did not reply, but the internal cutaneous in the upper arm was not obviously affected. Two areas of greatly diminished, but not abolished, reply were found, one on the outer side of the upper arm, the second on the anterior edge of the forearm. The latter was a well-defined oval patch, rather nearer the wrist than the elbow.

The evidence regarding the root-constitution of the dorsal and collateral digital nerves of the fore foot of the Cat, given by the above experiments, is tabulated below. It differs somewhat widely from the analysis by W. Krause (Rabbit) (4).

Cat. Fore foot.—Root-constitution of the collateral digital nerves.

No. of nerve-root.	Ist.	IInd.	IIIrd.	IVth.	Vth.	VIth.	VIIth.	VIIIth.	IXth.	Xth.	
VIth cervical . . .	+	+	?	..	..	..	..	..	..	..	Dorsal collat.
VIIth „ . . .	+	+	+	+	+	+	+	..	..	..	
VIIIth „ . . .	..	..	+	+	+	+	+	+	+	+	
Ist thoracic . . .	..	..	..	..	..	+	+	+	+	+	
VIth cervical . . .	+	..	..	..	..	..	..	..	..	..	Palmar collat.
VIIth „ . . .	+	+	+	+	+	+	..	..	..	..	
VIIIth „ . . .	+	+	+	+	+	+	+	+	+	+	
Ist thoracic . . .	..	..	..	..	..	+	+	+	+	+	

As the present paper deals only with the thoracic and post-thoracic spinal roots, regarding the root constitution of the collateral digital nerves of the fingers of *Macacus rhesus* it will suffice here to notice how far into those nerves the Ist thoracic root enters, as evidenced by the four experiments quoted above. With the VIIIth and Ist undivided a reflex was easily evoked from all the digitals, both dorsal and palmar, and VIIth contributes, *contra* Krause, at least to Ist and IInd dorsal and palmar collaterals. There seemed to be a contribution by the Ist root as far as Vth, perhaps IVth, collateral. The IInd thoracic root, although it gives motor fibres to the muscles in the hand, does clearly from the above experiments contribute no sensory fibres to the skin of any of the fingers or to any part of the hand itself.

Experimental Series II.

From these observations on Cat and *Macacus rhesus* it appeared clear that each branch of many of the sensory nerve-trunks in the limb consists of fibres which enter the cord by two or three distinct posterior roots, and that, therefore, just as there is a great interlapping of the limb territories of adjacent spinal nerve-roots judged by their distribution to the skeletal muscles, so also a great interlapping is evidenced in the distribution of the afferent fibres from the skin. It was also clear that as in the afferent roots of the Frog, so also in Cat and Monkey, some amount of individual variation is frequent. Points of interest especially requiring confirmation as unexpected and not in harmony with the observations on the Frog, or with the scheme of distribution of efferent fibres of the plexus, were the following. Among the conclusions arrived at from the experiments on the Frog is this: the cutaneous field for each posterior root meets the middle line of the body both ventrally and dorsally. In the Cat and Monkey after the above analysis of the constitution of the peripheral branches of the plexus it was clear the skin field of post-thoracic root VI could not possibly attain the dorsal or the ventral lines, it seemed roughly speaking to be distributed entirely to the apex of the limb—again, in the scheme of distribution to the musculature of the limb, the most segmentally posterior of the rays composing the limb penetrates to the very apex of the limb, both in the arm and leg. To judge from the above experiments this does not appear true for the segmental constitution of the *skin* of the limb. The posterior root of the VIIIth nerve does not appear to penetrate so far into the limb as does that of the VIth. That is to say, the limb being considered as a fin-like appendage, the musculature has a posterior border which is straight and abrupt, and formed out of one ray, the overlying skin has a posterior border which is slanting and gradual and composed of more than one ray. Again as regards the musculature it was often the case (in the post-fixed type of plexus) that root IX contributed well to the innervation of the limb. This root does not (according to the above experiments) contribute to the skin of the limb proper; therefore the skin to which it supplies afferent fibres and the muscle to which it supplies motor fibres are separated by nearly the whole length of the limb, breaking the rule set down by VAN DER KOLK,* PEYER (2), KRAUSE (4), and others. In order to obtain a clearer answer on these points I attempted a direct delimitation of the spinal sensory root-fields in the Mammal, in the same way as in the already cited experiments on delimitation of the root-fields in the Frog. An essential feature in these experiments consisted in severance of a sufficient number of nerve-roots immediately above and below the root examined to make a field of anæsthesia, on which as on a blank surface the territory of the æsthesia subserved by the isolated root could be mapped. The preparatory procedure of experiment was the same as for the observations on the root-composition of the various peripheral nerves, but of course no exposure of peripheral nerves was employed or necessary, mechanical excitation of the skin being substituted for mechanical and electrical excitation of the nerve trunks. The same recording method was employed in the Frog's experiments; that is, each point of the previously shaved skin that gave a reply was marked (with ink) at the time, and no other points were ever marked. After the whole area had been once explored in this way, a process which might occupy two or three hours, the extreme limit of the area was indicated by a white line carried on from reply spot to reply spot. After an interval of perhaps an hour this boundary-line was then very carefully and minutely explored at about 5-minute intervals, and the first white line was thus corrected as regards its detailed contour. After a few experiments on certain roots, especially root VI, it became evident that in this way a fairly constant figure was arrived at for the same root, subject to comparatively minor variations; it also became evident that the root distribution was such that in order to isolate one root-territory, in some cases so many as seven consecutive posterior roots above or below had to be severed. Some time and labour was wasted by my not recognizing this fact early enough, and its explanation will be dealt with after relating the experiments in which it occurred.

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* FRORIEP's 'Notizen.' 3rd series. 1847.

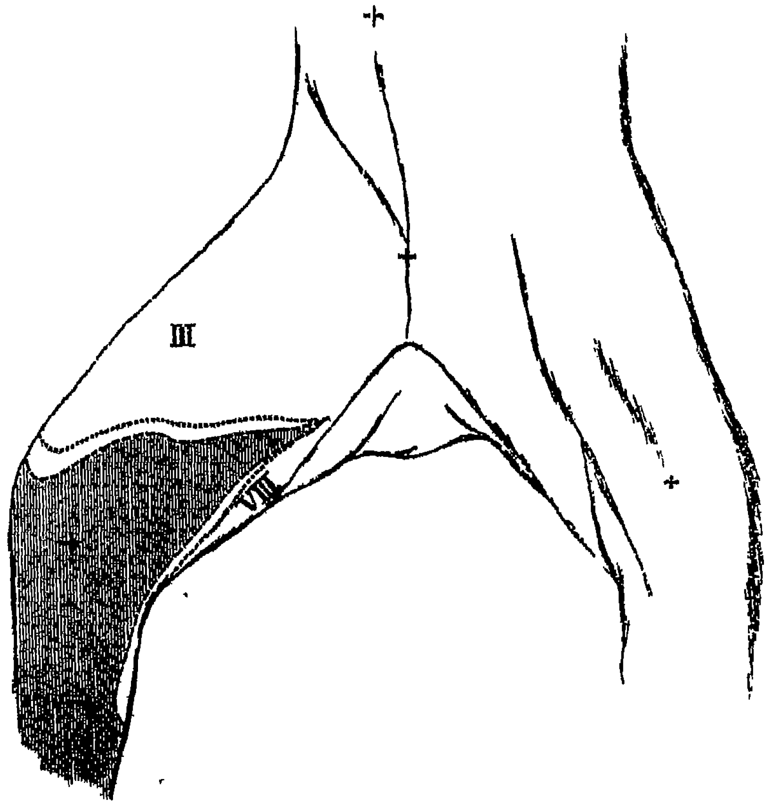
Regarding the form of stimulus used, the skin was pinched with a fine pointed pair of dissecting forceps, and sometimes a mere touch sufficed to elicit a reflex; at other times, especially near the edge of the root territory, a hard pinch had to be employed. At first I attempted to keep a record of the areas obtained by transferring them to "proportional paper" as in mapping from the microscope by means of the movable stage and squared eye-piece: difference of size and proportion, between individual and individual frustrated this attempt, the maps becoming too confusing from necessary absence of perspective and inability to follow accurately the two superficial dimensions of a very irregular solid figure. I then proposed to content myself with accurate measurements from comparatively fixed points and written description, illustrated with pencil sketches; the difficulty of obtaining accuracy with the latter, induced me to record with photography at the latter part of each experiment or immediately after it. As it was found that for photography in winter in London the ink marks often did not show up sufficiently on the pigmented skin, in the later experiments the boundary of the territories was usually indicated by a double line of white and black, the white border turned toward the side which yielded reflexes, the black toward that which did not yield reflexes. Finally plaster casts of *Macacus rhesus* were made under my own direction by Messrs. BRUCCIANI, and the position of the chief bony points accurately transferred from the individual whence the casts had been taken to the casts. Then the territory of the nerve-root desired to be transferred to the plaster model was delimited on an individual of approximately the same size as the cast, and in that way the model was gradually covered with the pattern of the various root territories. It was only when that had been done that certain important points in the scheme of their arrangement became salient. Several reasons led me beyond the limits of the lower limb in this part of the research.

In the series of experiments in which analysis of peripheral nerves into their root-composition was attempted by electrical excitation of the nerve and successive sections of the contributing roots, it was usually found that when one of the roots that contributed largely to, for instance, a small digital collateral nerve, had been severed, a very weak reply or no reply could be evoked from the proximal end of the digital nerve for a few minutes immediately subsequent to the section of the root; but if tested about twenty minutes later it gave a better reply, or even a smart reply, when previously there had been none. At first I imagined this the result of some adventitious error in the excitation. Later, one recognized the phenomenon as in some degree or other of constant occurrence. The same phenomenon has recurred in the last quoted series of experiments in which instead of analysis of nerve-twigs under electrical excitation, analysis of root-fields under mechanical excitation, has been the method. If the isolated *field of response* was delimited very soon after the posterior roots immediately above and below that distributed to the root-field under examination had been severed, a field was obtained of the approximate shape of the true root-field but smaller than it, and curtailed especially in certain directions. When examined later, the field of response, determined by exactly the same method as before, was found to have extended. The following instances exemplify this phenomenon.

Experiment.—*M. rhesus.* 20.10.1890.

The Vth, VIth, VIIth, IXth, and Xth roots (posterior) of the post-thoracic region severed on the right side, at 10.50. At 11 o'clock the delimitation of the areas carried out first. At 9.30 P.M. the delimitation of the areas carried out finally. The lower limit of the VIIIth root field has travelled downward 3·5 centims., that of the IVth about 1·4 centims. at greatest. The upper limit of the VIth and VIIIth root fields combined had advanced about ·8 centim. toward the perineum at greatest.

Fig. 3.

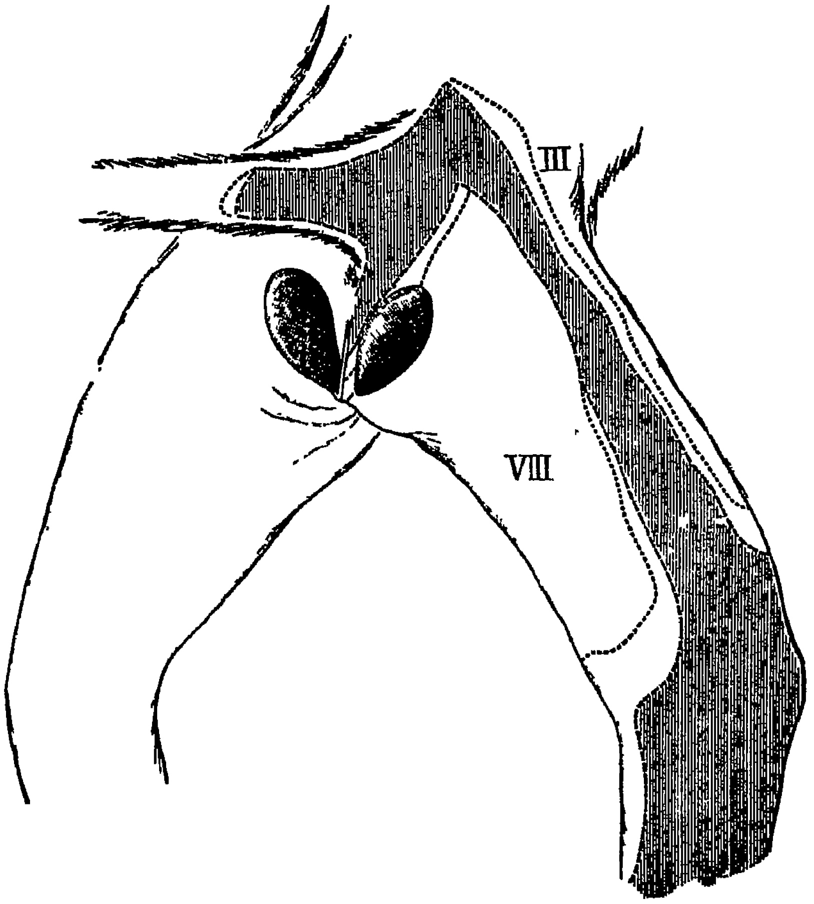


Experiment.—*M. rhesus.* 4.5.1891.

The posterior roots of the IVth, Vth, VIth, VIIth, IXth, and Xth post-thoracic spinal nerves of the right side severed in the spinal canal at 9.10 A.M. At 9.20 the delimitation of the field of the VIIIth post-thoracic root was carried on. The result was that the lower margin was placed distinctly above the flexure of the knee. (See figs. 3, 4, sketches made at the time.) At 4 o'clock the field of the VIIIth root was delimited again, and without hesitation the lower margin of the area was placed distinctly [illegible] the flexure of the knee and in part for a certain distance below it. (Figs. 3 and 4, the same sketch [illegible] upper margin had also extended, but not so far, in the direction of the perineum and [illegible] of the vulva. It was especially noticeable that there had been no obvious extension along the border turned toward the field of the IIIrd lumbar. That is to say, the advance had been confined to the anterior and posterior borders of the root field and had occurred but little at the dorsal and ventral borders. (See Conclusions, *infra*, p. 742.)

The second of the two experiments quoted was performed to determine the nature of the "extension of the field" in regard to the two borders, and the rate of extension at different periods; regarding the latter point it was found that the rate of "extension" was greatest in the first half-hour, and that in the third hour and afterwards there was little if any further progress of the field. I have been used to call the initial lowering of response, the "local spinal depression," and the subsequent increase of response and the accompanying increase of the area of reply, the "local spinal exaltation," and the "extension of the field." During the period of "local spinal depression" the responses besides being enfeebled are often of curiously long latency. The period of "local spinal depression" has often seemed to me to be shortened in duration by repetition of excitations, even when these are at first inefficient to evoke obvious responses.[*] The whole phenomenon appears quite comparable to the transient depression and subsequent exaltation of the "knee jerk" produced in, for instance, the Cat by section of the spinal cord above the lumbar region. And the briskness of the "jerk" may in like manner be increased by section in the spinal canal of the spinal roots, either sensory or motor, adjacent to that one most intimately concerned with the jerk, and especially of the

Fig. 4.



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[*] An example of the physiological process called by EXNER "Bahnung," PFLÜGER'S 'Archiv f. d. ges. Physiol.,' vol. 28, p. 487.

muscular nerves to the antagonists of the "jerk" muscles. In the field of a root immediately above severed roots, or immediately below severed roots, a marginal area of unmistakably exalted reflex reply is sometimes found. This is due, I imagine, to the "local spinal exaltation" and is an evidence of the local character of the exaltation. It may be essentially the same phenomenon as the hyperæsthetic zone bordering a paralyzed area (Fodéra, 1823*) after lesions of the spinal cord itself. The "local spinal exaltation" is of great assistance to the above method of delimiting the cutaneous spinal root fields; the whole field of the root isolated by sections of adjacent roots is more or less affected by the exaltation. In one of the experiments in which one half the rootlets of the posterior division of the VIth lumbar spinal root were cut through after previous section of the adjacent roots, it seemed clear that in the plantar region the reflex response was *increased further* after the section of half the rootlets of the spinal root. As to the length of time which the phenomenon lasts I can say little, but the exaltation of the knee jerk after section of adjacent roots I have seen persist for more than three months. Of course it must be remembered that in that case the loss of the tone of the muscles antagonistic to those on which the jerk depends may play a main part in the production of the exaggeration of the jerk. The influence of a sensory root on the activity of the motor, or of blocking one motor root on the activity of another, is too far from the present experiments to be entered upon here, but I have attempted to see whether the "local spinal depression" could be demonstrated to affect the reaction of the anterior root to cortical excitation, and I have not been able to show that it does. Two experiments were made with a similar result, which evidenced rather local exaltation than depression.

Experiment.—*M. rhesus.* Female. 11.2.1891. A.C.E. mixture. Cord exposed in the canal.

11.25 A.M. Excitation of central end of each of three filaments (about 4 centims. long) of the posterior root of the Vth post-thoracic nerve elicited reflex movements (secondary coil at 39 centims. from primary: Ewald's inductorium with 1 Daniell), slight eversion of foot, followed by slight adduction and flexion of hallux, rarely followed by abduction and slight extension of hallux. Each of the filaments when strength of excitation is increased gives flexion at hip (*i.e.*, drawing up of knee), no extension of knee, but some extension at ankle, and in digits and hallux. The most marked feature of the reflex with all the strengths (from 39 centims. to 25 centims.) was the action of the peronei.

11.50. Left "motor" cortex exposed. Excitation at the top of the central sulcus gave movements of the hallux, and, with stronger excitation, of the foot. The movements of the hallux sometimes extension, sometimes flexion.

12.20. The posterior roots of the VIth, VIIth, VIIIth, and IXth post-thoracic nerves of the right side have silk thread carefully slipped under each. (Vth root already cut.)

12.28. The central ends of the three filaments excited each as before; each gives similar reflex reply, and the replies are not distinguishable from those obtained before.

12.42. Cortex excited. Flexion of hallux obtained with minimal current (secondary coil at 17 centims.)

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* Magendie's 'Journal de Physiologie,' vol. 3, p. 191.

12.46. Cortex excited once at same spot. Same movements obtained with secondary at 17 centims. Coil at 18 not effective.

12.48. The posterior roots of the VIth, VIIth, VIIIth, and IXth post-thoracic nerves all rapidly cut through with scissors (in about 40 seconds).

12.54. Cortex excited at same spot as before (coil at 17 centims. from primary) gives as brisk movement of hallux (flexion).

12.59. Cortex for hallux and fingers responds to excitation at 19 centims.

1.4. Cortex for hallux responds at 19 centims. Reply is brisker than before.

1.10. Cortex for hallux responds at 21 centims.; at 20 hallux and fingers both respond well.

On February 23 a similar experiment was made, with the same result.

In describing the experiments the use of a few special terms is unavoidable:—

The *mid-dorsal line of the body* to denote the middle line of the dorsal surface of the animal, the surface consisting of right and left halves, which meet at the mid-dorsum.

The *mid-ventral line of the body* to denote in a similar sense the middle line of the ventral surface of the animal.

The *mid-lateral line of the body* to denote a line of surface equidistant from the mid-dorsal and mid-ventral lines of the body.

The mid-dorsal and the *mid-ventral lines of the limb* are lines on the limb surface, along which the skin fields of the sensory roots behave as if at the mid-dorsal and mid-ventral lines of the body. See Plate 52.

The *dorsal border* of the skin field of a root is that border which follows the mid-dorsal line; the *ventral border* that border which follows the mid-ventral line.

The *anterior border* of the skin field is that border of the field which runs between the most anterior (headward) point of the dorsal border and the most anterior point of the ventral border. The *posterior border* of the skin field runs between the most posterior point of the dorsal border and the most posterior point of the ventral border.

(For *anterior* and *posterior overlapping* and *dorsal* and *ventral crossed overlapping*, see p. 652 *supra*, and Plate 52.)

The experiments are arranged in an order that traces the distribution of the posterior roots in series from before backwards on the long axis of the body.

Ist Thoracic.

Experiment.—*Macacus rhesus*. Female. 22.6.1891.

At 11.10, the posterior divisions of the Vth, VIth, VIIth, VIIIth cervical and IInd, IIIrd, and IVth thoracic nerves of the right side divided in the spinal canal. At 4.30, the isolated region of reply (*i.e.*, of *Ist thoracic*) delimited finally.

"The isolated field of response is bounded by a line that is traceable from the ulnar side of the proximal phalanx of the middle digit, backward and upward over the knuckle of that digit to the back of the lower end of the radius over the tendon of the extensor carpi radialis brevior; thence the line advances toward and reaches the radial edge of the forearm at junction of middle and lowest thirds; then it slopes toward the ulna, and, in the highest third, runs straight up, so as to lie midway between the external condyle and the skin-fold over the biceps insertion. At the level of the head of the radius, the line turns abruptly backward passing about ·5 centim. above the outer condyle round to just above

(3 millims.) the olecranon. Winding round the olecranon at a point 1 centim. above the internal condyle, it then turns sharply upward, ascending on the axillary aspect of the arm about 1 centim., or less, behind the biceps (on the triceps side) to a level with the deltoid insertion; at that place it recurves upon the biceps, and, winding round that muscle, slants down first on the inner face, and then on the front of the belly of the muscle, so as to pass into the hollow to the ulnar side of the supinator mass at the flexure of the elbow. It then tends at first a little in the direction of the ulnar edge, and soon runs down the middle of the flexor aspect of the forearm to enter the palm, crossing the wrist in the groove between the thenar and pisiform eminences. It finally reaches the flexor aspect of the proximal phalanx of the middle finger a little toward its ulnar side, and then attains the point it started from."

Measured:—

Suprasternal notch to infrasternal	9	centims.
„ „ mammilla	4·5	„
„ „ umbilicus.	18·5	„
„ „ pubic crest	26	„
Acromion to tip of 3rd digit	31·5	„

Twelve ribs each side. No extra mammillæ.

Ist Thoracic.

Experiment.—*Macacus sinicus.* Male, young. 25.5.1891.

Measures:—

From suprasternal to infrasternal notch	6	centims.
„ „ „ crest of pubes	22	„
„ head of humerus to tip of 3rd digit	26·5	„
„ nipple to infrasternal notch	4	„

At 10.30, the posterior divisions of the VIth, VIIth, VIIIth cervical and the IInd, IIIrd, IVth, and Vth thoracic spinal nerves of the right side divided in the spinal canal. At 2.10, delimitation of field of response completed.

"The line then turns back over the olecranon, and outwards to the point of the outer condyle, and across in front of the brachial fold to outer edge of biceps just above its insertion; it then bends sharply and runs down toward the hand, sloping outwards so as to cross the outer surface of the radius a little below the middle of that bone. It crosses the wrist about midway between the radial and ulnar styloid processes and bisects the back of the hand. It then curves outward to reach the base of the little finger. It enters the palm over the web between 5th and 4th digits, and runs upward curving outward so as to include the inner third of the thenar eminence. At the front of the wrist it lies a little to the radial side of the middle. It keeps somewhat to the radial side of the middle line of the forearm to the skin over the outer side of the insertion of the biceps tendon."

In this experiment, the field of the Ist thoracic was not distinguished from the field of the Vth cervical, but the separation is easy in the light of subsequent experiments, as the two fields are only apposed over a little space.

Twelve ribs each side.

IInd Thoracic.

Experiment.—*M. rhesus.* 5.8.1891. Plate 42, fig. 1.

Measurements as on p. 699.

At 12.30 the Vth, VIth, VIIth, VIIIth cervical, the Ist, IIIrd, IVth, Vth, VIth thoracic roots of the right side divided.

[illegible] delimitation of the skin field of the IInd thoracic root.

[illegible] is not perfectly isolated, it joins, by a band of low irritability, the upper field of reply" (IVth cervical). "The extent of this imperfect fusion of the two fields measures about 2·5 centims. The posterior edge of the isolated field must be the edge that is nearest the spine at the junction with the lower edge of the upper field of reply, and that junction is over the triangular subcutaneous piece at the root of the spine of the scapula. From that place the edge descends first, and then runs outward over the infraspinous fossa at 1 centim. above the inferior angle of the scapula, and then along the posterior fold of the axilla to the upper arm, reaching the actual crest of the ridge of it at the angle of junction of the arm and trunk (at the shoulder). It then tends down the thoracic wall a little way forming a shallow, broad tongue, and runs down the arm again, crossing to the biceps side of the axillary groove of the upper arm, and nearly coming in contact with the upper field on the upper part of the belly of the biceps." "Close below the lowest point to which the field attained on the arm was a little oval area about 2·5 centims. long, which gave replies, and yet could not be clearly shown to actually be continuous with the main area. This islet was the lowest point to which the field attained on the limb."

Normal number of ribs (twelve) each side, verified by *post-mortem* examination.

IInd Thoracic.

Experiment.—*M. rhesus.* Female; strong. 18.6.1891.

Dimensions as on p. 699.

At 11.30 A.M. the IIIrd, IVth, VIth, VIIth, VIIIth cervical, and Ist, IIIrd, IVth, and Vth thoracic roots of the right side severed.

At 6.10 the lower of the isolated fields of reflex reply finally delimited (*i.e.*, the field of the IInd thoracic root).

"The boundary of the lower of the isolated fields of reply extends from a point one-third down the forearm at the junction of the ulnar and flexor aspects, thence upwards, sloping across the subcutaneous surface of the root of the olecranon, and up the space between the olecranon and the inner condyle. Thence it passes up the upper arm along the middle of its posterior aspect on the subcutaneous surface of the triceps just behind the biceps and just behind the deltoid muscle, to meet the spine of the scapula at its junction with the root of the acromion; and then returns, and soon recurves upward again, and retires again. It thus leaves a Y-shaped piece with a double tongue, each tongue about 2 centims. wide, the upper passing across the axillary border of the scapula, to as far as the scapular spine, the lower not quite reaching that retiring scapular edge, but getting to within less than a centimetre of it. The lower tongue runs, in fact, down the fold of muscle covering the scapular edge, and turns up upon it again, so that it follows the posterior fold of the axillary space for a certain extent, and comes down the upper arm in the groove, or a little behind the groove between the triceps and biceps muscles. It so comes to lie in front of, *i.e.*, on the flexor face of, the muscular origins from the inner condyle, and then reaches the point it was traced from about one-third down the forearm."

The normal number of ribs present. Two pairs of nipples.

IInd Thoracic.

Experiment.—*M. rhesus.* Female; strong. 10.6.1891.

Dimensions:—

Suprasternal notch to pubic crest . . .	30	centims.
" " infrasternal notch .	10	"
" " nipple	4·5	"
Acromion to tip of 3rd digit	28	"

At 9.10 the IIIrd, IVth, Vth, VIIth, and VIIIth, and the first two thoracic roots of the right side severed.

At 5.30 the anterior border of the field of the IIIrd thoracic finally ascertained.

"The upper edge of the lower field of reply runs from the ventral cross-lap 2 centims. above the intermammillary line, horizontally outward over the nipple to the pectoral fold 2 centims. from the arm; along that fold it descends upon the biceps, then on to the coraco-brachialis, to slope out to the triceps about 2 centims. above the flexure of the elbow; it descends to the top of the elbow in a straight line, and passes up again, at first between the outer and middle portions of the triceps, to strike the outer edge of the scapula half way up it. It passes over the junction of the base of the spine of the scapula with the triangular space at the root of the spinous process, and then slopes down and inward. It leaves the vertical edge of the scapula at the above-mentioned triangular space, and meets the mid-dorsal line about on a level with the mammilla, or somewhat lower than that."

Twelve ribs existent each side.

IIIrd Thoracic.

Experiment.—*M. sinicus.* Young male. 28.5.1891.

Measured:—

Acromion to tip of 3rd digit .	29 centims.
Sternum	8·8 „

At 8.50 the VIIIth cervical, the Ist, IInd, IVth, Vth, VIth, and VIIth thoracic roots (posterior roots) of the right side severed.

At 5.10 the final delimitation of the field of reply due to the IIIrd thoracic root.

"The lower edge of the almost isolated field of response can be traced from a ventral crossed overlap on the sternum about 5 centims. below the clavicle, and from that point slants outward and upward to cross the nipple line about 0·4 centim. below the nipple. It then runs, if the arm be extended at right angles to the trunk, in a slightly ascending direction as far as the mid-axillary line. It then slightly descends so that its lowest point is where it sweeps round the posterior axillary fold. After that it runs horizontally across the inferior angle of the scapula (arm horizontally extended to a point about 2 centims. from the mid-dorsal line). Thence it abruptly turns upward to reach the lower border of the scapular spine at the medial edge of the scapula. It runs along the lower border of the spine of the scapula outward, descending slightly below it at its outer end. It reaches a point half way between the tip of the acromion process above, and the lower border of the triceps at the junction of the arm and shoulder. At that point it meets another line limiting the upper field of reflex response. Parallel with this line it descends the back of the upper arm to within 2 centims. of the olecranon; at that distance from the elbow it curves inward and then returns up the arm along the inner edge of the triceps mass. It passes upward and inward across the thoracic wall of the axilla. Finally, on the border of the pectoral fold it meets again the lower limit of the upper field of response, and is not further isolated from it."

IIIrd Thoracic.

Experiment.—*M. sinicus.* Female, young. 26.8.1891. Plate 42, fig. 2.

Measurements:—

Length of arm from acromion to tip of 3rd digit	23 centims.	
From suprasternal notch to pubic crest	21·5 „	
„ „ umbilicus	14 „	
„ „ mammilla	4 „	(obliquely)
„ „ infrasternal notch	7·4 „	

[illegible] the IVth, Vth, VIth, VIIth, VIIIth cervical, the Ist, IInd, IVth, Vth, and VIth thoracic [illegible] divided.

At 5.30 the cutaneous field of the IIIrd thoracic delimited finally.

"The upper edge of the isolated field of reply extends from the mid-ventral line 1·5 centim. below the lowest edge of the upper field of reply" (IIIrd cervical) "that is 2 centims. above the nipple horizontally outward for 2·5 centims. till it meets the anterior axillary fold. It then runs parallel to that fold, but on the anterior surface of the pectoral eminence about 0·3 centim. above that fold. It then turns down the biceps (inner edge), probably on the coraco-brachialis to the bicipital space (inner edge) nearly as low as a line joining the condyles of the humerus. It retires 0·5 centim. and then winds round the inside of the arm about 1 centim. above the inner condyle, reaching the posterior surface of the arm 1 centim. above the olecranon (arm extended). The line then abruptly ascends the arm on the triceps fold rather nearer the lower than the upper border of the arm (arm horizontal). It enters the infraspinous fossa about half way up the axillary border of the scapula, and reaches the posterior edge of the scapula just below the triangular subcutaneous piece at the base of the spine of the scapula. It then turns at an acute angle outward, and crosses the infraspinous fossa to the outer border, which it reaches close above the inferior angle of the scapula; it ascends again a little distance, winding round the scapular fold and crossing the thoracic wall of the axilla above the level of the nipple, but always slightly descending; it then winds round the thorax, sloping slightly downward and passing about 0·2 centim. below the nipple to reach the mid-ventral line."

IIIrd Thoracic.

Experiment.—*Macacus rhesus.* Female. 6.4.1891.

Dimensions:—

Head to 3rd digit, point of .	11	centims.
Nipple to sternal notch . .	4	„
Ankle to knee	13	„
POUPART's ligament to knee	11·5	„

At 10.30 the roots of the IVth, Vth, VIIth, and VIIIth thoracic nerves of the right side divided in the spinal canal.

At 3.20 the lower border of the field of the IIIrd thoracic root determined.

"The lower edge of the upper field of reply starts from the mid-dorsum somewhat above half way up the scapula; it slopes slightly downward as it passes outward, and, crossing over the infraspinous fossa of the scapula, turns the axillary border over close under the posterior angle of the axillary space, crosses the thoracic wall of the space and meets the pectoral fold a little above the level of the nipple. The line then runs horizontally above the nipple, passing just above it, to the ventral crosslap on the sternum."

IVth Thoracic.

Experiment.—*M. rhesus.* Female, strong. 22.10.1891. Plate 43, figs. 3 and 5.

Dimensions:—

From suprasternal notch to infrasternal . . .	9	centims.
From infrasternal notch to pubic crest. . . .	18·5	„

The IVth, Vth, VIth, VIIth, VIIIth cervical, and the Ist, IInd, IIIrd, Vth, and VIth thoracic roots of the right side severed at 11.15. At 7.30 the field of the isolated IVth thoracic finally delimited.

"The upper edge of the isolated field of reply passes almost horizontally from the mid-dorsal line to the border of the scapula at the lowest point of the triangular surface at the root of the spine of the scapula. It slopes a little downwards in crossing the scapula, and runs down the back of the arm as far as one-third the way to the olecranon. It there returns and enters the axilla, penetrating to the apex of the axillary space. It winds over the edge of the pectoral fold so as to reach its anterior aspect halfway between the origin and insertion of the thoracic part of the pectoralis major. From that place it slopes downward and meets the mid-ventral line on the sternum at the lower edge of the 2nd costal cartilage. It there lies nearer to the lower edge of the upper field of reply (IIIrd cervical root) than to the mammilla.

"The lower edge of the isolated field of reply passes from the mid-dorsal line, about 3 centims. below the point of commencement of the upper edge from that line. It slopes more steeply downward than does the upper edge, and therefore does not run parallel with it. It passes outward close below the inferior angle of the scapula. From that point, sloping less than it has done, it runs fairly directly toward the mid-axillary line. In that line it passes just below the lower border of the 5th rib. It then ascends somewhat, and runs more horizontally to meet the mid-ventral line on the sternum at the upper border of the sternal end of the 5th costal cartilage. Its distance from the nipple in the vertical of the nipple is 1·5 centim. (below it).

"The nipple is situate, when measured on the cage of the thorax (by transfixion), midway between the apices of the 2nd and 3rd ribs. After the above field has been delimited it is seen that the nipple lies in it about midway between the anterior and posterior edges of the field.

"The field reaches its greatest vertical depth about 2 centims. in front of the inferior angle of the scapula, where, when the tongue-shaped extension down the arm is included, it has a breadth of 7 centims. The field is shortest at the mid-dorsal line, where it measures 2·5 centims. It is next narrowest at the mid-ventral line, where it measures 3 centims."

IVth Thoracic.

Experiment.—*M. rhesus.* Female. 2.6.1891.

Dimensions when the arm is extended at right angles to the trunk :—

Suprasternal notch to crest of pubes .	23	centims.
Acromion to top of 3rd digit	26·5	,,
Infrasternal notch to suprasternal . .	7·1	,,
,, ,, mammilla . . .	4·5	,,
Suprasternal notch to mammilla . . .	3·5	,,

At 9.5 the IVth, Vth, VIth, VIIIth cervical, and the Ist, IInd, and IIIrd thoracic roots of the right side severed. At 4.10 the upper edge of the cutaneous field of the IVth thoracic fully ascertained.

"The upper edge of the lower field of reflex reply extends from the ventral crosslap on the sternum outwards, passing 1·5 centim. above the nipple, and reaching a point 3 centims. from the mid-ventral line, from which point it slopes upward and outward to cross the wall of the thorax in the axilla. It winds round the pectoral fold about midway up it, and passes on to turn downward inside the fold over the latissimus dorsi, and then bends backward on the inner head of the triceps about one-third the way down the upper arm. When it has attained the middle line of the posterior aspect of the upper arm, a little below the junction of the middle and upper thirds of the arm, it turns abruptly upward, and keeping to the crest of the triceps prominence it strikes the outer edge of the scapula rather more than a quarter up it. It passes across the scapula to the lowest point of the triangular space at the root of the scapular spine, and then it slopes downward to attain the mid-dorsal line at a level lower by 1 centim. to 2 centims. than the level at which it commenced when traced from the mid-ventral line; a level below the inferior angle of the scapula when the arm is extended horizontally."

[illegible] verified as normal at autopsy.

IVth Thoracic.

Experiment.—*M. rhesus.* Female; young. 17.12.1890.

Measured:—

Umbilicus to pubes	8·5	centims.
Nipple to pubes	21·5	„

At 11.30 the Vth, VIth, VIIIth, and IXth thoracic roots of the right side severed. Final delimitation of the border of the IVth thoracic at 5.20.

"The posterior (lower) edge of the upper field of reply extends from a point on the mid-dorsal line 12 centims. above the level of the anterior superior spine, and from that point passes almost horizontally outwards just below the inferior angle of the scapula (in the raised position of the arm) and slopes slightly downward over the lateral aspect of the chest, running 2 centims. under the nipple and reaching the mid-ventral line on the sternum, perhaps somewhat less than 2 centims. below the inter-mammillary line."

Ribs twelve in number in this individual.

Vth Thoracic.

Experiment.—*M. rhesus.* Female. 7.6.1891.

Measurements when arm is at right angles to trunk:—

Tip of middle digit to acromion		27	centims.
Suprasternal notch to	infrasternal	7	„
„ „	umbilicus	16	„
„ „	crest of pubes	24	„
„ „	mammilla	4	„

At 10.45 the IVth, Vth, VIth, and VIIth cervical, and the highest four thoracic nerve-roots, severed on the right side. The anterior border of the cutaneous field of the Vth thoracic, estimated finally at 7.15.

"The upper border of the lower field of reply runs from the ventral crossed overlap ·5 centim. above the nipple, horizontally outward to the anterior pectoral fold, then turns up that fold for about 1 centim. and down again to cross the thoracic wall of the axillary space about on a level with its point of origin. It then reaches the latissimus dorsi fold and runs round it in the angle of junction of the arm with the posterior axillary fold, and gets upon the scapula by crossing the axillary border of it at junction of the middle with the lowest third. The line strikes the spinal ridge of the scapula about ·5 centim. below the base of the spinous process. From that point it slopes downward to reach the mid-dorsal line 3 centims. lower, *i.e.*, about 1·8 centim. lower than the junction with the ventral crossed overlap."

Found, *post-mortem*, to have twelve ribs on each side.

Vth Thoracic.

Experiment.—*M. rhesus.* Female. 22.6.1891.

Measurements, with the arm horizontally extended:—

Suprasternal notch to	infrasternal	9·5	centims.
„ „	mammilla	4·5	„
„ „	umbilicus	18·5	„
„ „	pubic crest	25·5	„
Acromion to tip of middle digit		31·5	„

At 10 A.M. the lowest four cervical, and the IInd, IIIrd, and IVth thoracic roots severed on the right side.

At 4 A.M. the anterior border of the skin field of the Vth thoracic root finally delimited.

"The anterior border runs from the ventral crossed overlap, 3 centims. below the suprasternal notch, outward 1 centim. above the nipple, thence to the edge of the pectoral fold, and up that fold to pass on to the arm and follow the apex of the deltoid triangle round to the back, but about ·75 centim. below, *i.e.*, distal to the triangle, so as to extend very nearly half-way down between the acromion and the flexure of the elbow; thence the border turns upward following the deltoid, and then across the scapula, gradually approaching the ridge of spinous process, and over the triangular subcutaneous space at the root of that process, leaving the scapula on a level with the base of the spinous process, to descend slightly from that in a straight line to the mid-dorsal line."

VIth Thoracic.

Experiment.—*M. sinicus.* Male; young. 25.5.1891.

Measurements with arm extended horizontally:—

From suprasternal notch to crest of pubes	22	centims.
" " " infrasternal notch	6·5	"
" acromion to tip of 3rd digit	26·5	"
" nipple to infrasternal notch	3·25	"

At 2 P.M. the VIth, VIIth, and VIIIth cervical roots, and the IInd, IIIrd, IVth, and Vth thoracic roots severed on the right side. The anterior border of the cutaneous field of the VIth thoracic, finally examined at 8 P.M.

"The anterior edge of the lower field of reply runs from 1·5 centims. above the infrasternal notch, from a good 1 centim. crossed overlap, outwards and upwards to a little less than 1 centim. below the nipple in the nipple line; the edge then passes almost horizontally to 2 centims. behind the mid-axillary line, where it rises somewhat, and then sinks posteriorly, sloping backward to meet the mid-dorsal line just about the level at which it strikes the mid-ventral line in front."

At the autopsy twelve pairs of ribs were found.

VIth Thoracic.

Experiment.—*M. rhesus.* Female. 6.4.1890.

Measurements:—

Heel to tip of 3rd digit	11	centims.
Nipple to sternal notch	4	"
Ankle to knee	13	"
POUPART'S ligament to knee	11·5	"

The roots of the IVth, Vth, VIIth, and VIIIth thoracic nerves of the right side divided in the spinal canal at 10.35.

At 3.50 the field of the VIth thoracic root delimited.

"The lower edge of the isolated field of reply runs from the mid-dorsal line about 1·5 centims. above the inferior angle of the scapula outwards, and downwards out of the lower part of the infraspinous fossa to the side of the chest. It lies in the nipple line below the level of the infrasternal notch, and about 5 centims. below the nipple. It reaches the ventral crossed overlap 8·5 centims. above the umbilicus, which is rather further above the umbilicus than the umbilicus is above the pubic crest, and much nearer the level of the nipple than of the umbilicus."

[illegible] isolated field of reply extends from the mid-dorsal line a a point about

2·5 centims. above the point whence the lower limit starts. With very little curving it turns outward and slopes over the scapula across the thoracic wall of the axilla, to bend round the edge of the pectoral fold about 2 centims. below the level of the nipple, and cross at about that distance below the nipple to reach the ventral crossed overlap of the sternum at the base of the xiphoid process."

VIth Thoracic.

Experiment.—*M. rhesus.* Female; strong. 18.6.1891.

Measurements when the arm is extended horizontally:—

From suprasternal notch to infrasternal	8·5	centims.
„ acromion to top of middle digit	30·5	„
„ suprasternal notch to pubic crest	31·5	„
„ „ „ nipple	4	„

The following roots were severed at 11.30 A.M.:—The IIIrd, IVth, VIth, VIIth, and VIIIth cervical, the Ist thoracic, the IIIrd, IVth, and Vth thoracic on the right side.

Final delimitation of the anterior border of the skin field of the VIth thoracic at 8.30.

"From the ventral crossed overlap about ·5 centim. below the large uppermost thoracic nipple, about horizontally outward to the mid-point of the axilla; thence it ascends somewhat, and descends, passing backwards close below the inferior angle of the scapula, and thence horizontally inwards to the mid-dorsal line."

Post-mortem examination proved the ribs to be twelve in number. Two pairs of nipples, of which the upper corresponds with the pair usually present.

VIIth Thoracic.

Experiment.—*M. rhesus.* Female; young. 5.8.1891.

Measures:—

From suprasternal notch to crest of pubis . . . . 28 centims.

At 12.40 the following roots severed on the right side:—The Vth, VIth, VIIth, and VIIIth cervical; the Ist, IIIrd, IVth, Vth, and VIth thoracic. Final delimitation of the anterior border of the skin field of the VIIth thoracic was made at 9.30. The upper edge of the lower field of æsthesia passes from a point in the mid-sternal line on a level just below midway between the nipple and the infrasternal notch, and passing round 2·5 centims. below the nipple reaches the mid-dorsal line over the 4th dorsal vertebra.

Post-mortem examination found twelve ribs each side.

VIIth Thoracic.

Experiment.—*M. rhesus.* Female; young. 17.12.1890. Plate 43, fig. 4.

Measured:—

Umbilicus to pubes	8·5	centims..
Nipple to pubes	21·5	„

At 11.30 the Vth, VIth, VIIIth, and IXth thoracic roots of the right side severed.

Final delimitation of the border of the VIIth thoracic at 6.30.

"The anterior edge of the isolated field of reply passes from a point in the mid-sternal line about 6 centims. below the nipple, outwards, and somewhat rapidly upwards, to cross the nipple line 3·5 centims. below the nipple, and after extending horizontally, again sweep upward so as to reach a level about 2 centims. below the nipple level, and thence run almost horizontally inwards to the mid-dorsal line, which it attains at a point about 2·8 centims. anterior to the point at which it joins the mid-ventral line."

"The posterior edge of the isolated field of reply passes from a point in the mid-ventral line very nearly 6 centims. above the umbilicus, and runs outwards, slightly ascending, and crossing the edge of the cage of the thorax at the tip of the 9th costal cartilage. It crosses the line of the deepest vertical of the cage of the thorax on the 10th rib, and making a gradual ascent in its course reaches the mid-dorsal line about 2·8 centims. behind the anterior edge of the field."

"The distance of the posterior border of the upper field of reply (IVth thoracic) from the anterior edge of the isolated field of reply is greatest (2 centims.) near the mid-ventral line, least somewhat on the ventral side of a vertical drawn upward from the anterior superior spine of the iliac crest, and is there about 5 centims. The distance of the posterior border of the isolated field of reply from the anterior edge of the lower field of reply (the Xth thoracic root-field) is greatest close to the mid-venter and is there 2 centims., and is least in the vertical drawn upward from the anterior superior spine of the ilium, where it is only ·4 centim."

"The dorsal border of the isolated field of reply comes quite up to the lip of the incision made at the commencement of the operation, that is to say, laps across the mid-dorsal line by at least 5 millims. The dorsal border measures 2·6 centims. The ventral border of the field measures about 3 centims. but has rounded angles, it laps across the mid-ventral line by more than ·5 centim. at places."

"The isolated field of reply is a band stretching from mid-dorsal line to mid-ventral line, its narrowest part is at the dorsal edge, and its widest part is about the middle of the lateral aspect of the chest where its measurement is 3·8 centims."

At autopsy the pairs of ribs were twelve in number.

VIIth Thoracic.

Experiment.—*M. rhesus.* Male; strong. 27.11.1890.

Measures:—

From umbilicus to pubic crest	9·3 centims.
,, nipple to pubes	22·8 ,,
,, xiphoid to umbilicus	10 ,,

At 12.15, the VIIIth, IXth, Xth, and XIIth thoracic, and the Ist, IInd, IIIrd, IVth, Vth, VIth, and VIIth lumbar nerve-roots divided on the right side. At 5.45 the final delimitation of the posterior border of the cutaneous field of the VIIth thoracic root.

"The lower limit of the upper field of reply crosses from the mid-dorsal line over the lateral aspect of the chest about 2·5 centims. above the lowest point of the thoracic cage. It leaves the thorax just above the tip of the 9th rib, and strikes the mid-ventral line half-way between the ensiform cartilage and the umbilicus, *i.e.*, 5·4 centims. above the umbilicus."

VIIth Thoracic.

Experiment.—*M. rhesus.* Female; strong. 22.10.1891.

Measures:—

From suprasternal notch to infrasternal	9 centims.
,, pubes to infrasternal notch . . .	18·5 ,,
,, ,, ,, . . .	18 ,,

At 11.15 the lowest five cervical and the Ist, IInd, IIIrd, Vth, and VIth thoracic roots of the right side severed. Anterior edge of skin-field of VIIth thoracic finally examined at 6.10.

[illegible] upper border of the lower field of æsthesia starts from the mid-dorsal line 2·5 centims. below the lower edge of the cutaneous isolated field (proved by *post-mortem* dissection to be the IVth thoracic) runs outward more horizontally than does that, and very accurately parallel with the upper edge of the isolated field. Under the inferior angle of the scapula the edge is only 8 millims. below the lower edge of (IVth thoracic) isolated field, and runs parallel with that to the mid-axillary line, where it slopes downward more and reaches the mid-sternum nearly 2 centims. below it at the level of the upper edge of the 7th costal cartilage at its sternal end. This upper limit of the lower field of æsthesia is at a lateral distance of one inch from the mid-dorsal line on a level with the angle of rib 8, and runs almost horizontally toward the spine. The tip of the spinous process of the 8th thoracic vertebra is just about on the same horizontal level, or perhaps a trifle lower than the angle of the 8th rib."

"In the dorsal portions of the lower and the isolated cutaneous fields, the anterior border runs more horizontally than does the posterior border of the isolated field. In the ventral portions of the fields the anterior border descends, *i.e.*, slants off posteriorly more rapidly than does the posterior of the isolated field."

Ribs, twelve in number each side.

VIIth Thoracic.

Experiment.—*M. sinicus.* Female; young. 26.8.91. Plate 42, fig. 2.

Measured :—

Acromion to tip of 3rd digit	23 centims.
Suprasternal notch to pubic crest	21·5 ,,
,, ,, nipple	4 ,,
,, ,, infrasternal notch . .	7·5 ,,

The posterior divisions of the IVth, Vth, VIth, VIIth, VIIIth cervical, the Ist, IInd, IVth, Vth, and VIth thoracic roots of the right side divided (in the vertebral canal) at 8.50. At 4.30 the cutaneous field of the VIIth thoracic delimited at its anterior border.

"The edge of this field agrees closely with the edge found on the 8th of this month in *M. rhesus.* It sweeps below the nipple (2·75 centims. below) from a point on the mid-sternum a little more than half-way from the nipple to the xiphoid notch."

Post-mortem examination showed twelve pairs of ribs.

VIIIth Thoracic.

Experiment.—*M. sinicus.* Male, young. Testes undescended. 28.5.91.

Measurements :—

Suprasternal notch to infrasternal notch . . .	8·8 centims.
,, ,, pubic crest	27 ,,
Acromion to tip of 3rd digit	29 ,,
Nipple to infrasternal notch	4 ,,
,, suprasternal notch	4·5 ,,

At 8·50 the VIIIth cervical and the Ist, IInd, IVth, Vth, VIth, and VIIth thoracic roots of the righ side severed. At 6.15 the anterior border of the cutaneous field of the VIIIth thoracic finally ascertained.

"The anterior edge of the lower field of reply starts from a good 1·5 centim. of crossed overlap on the sternum, at a level about ·5 centim. above the sub-thoracic notch, and then slopes upward to cross the mammillary line 3 centims. below the mammilla; it curves upward and then boldly descends behind the mid-axillary line so as to cross the 7th rib at a level rather below that of the junction with the ventral crossed overlap. It then runs horizontally back to the mid-dorsal line, with a dip of ·75 centim., half-way between the posterior axillary line and the mid-dorsal line."

On *post-mortem* examination, thirteen ribs were found on each side.

VIIIth Thoracic.

Experiment.—*M. rhesus.* Female. 8.6.1891.

Dimensions:—

Middle of POUPART's ligament to nipple	19·5	centims.
" " " edge of tibial head	10·5	"

At 8.50 A.M. the roots of the IXth and Xth thoracic nerves of the right side severed in the spinal canal. At 1.15 the posterior border of the cutaneous field of the VIIIth thoracic root determined.

"The lower edge of the upper field of reply slopes from the mid-dorsal line on a level with the inferior angle of the scapula (the arm raised above level of shoulder) and runs downwards and forwards about 1 centim. below the scapula; it passes over the ventral edge of the cage of the thorax above the point of the 10th rib, and about 10·5 centims. above the middle of POUPART's ligament. It reaches the ventral crossed overlap 4·6 centims. above the umbilicus."

IXth Thoracic.

Experiment.—*M. rhesus.* Female. 6.4.1891.

Measurements:—

Nipple to sternal notch	4	centims.
Ankle to knee	13	"
POUPART's ligament to knee	11·5	"

At 10.30 the IVth, Vth, VIIth and VIIIth thoracic nerve roots of the right side divided in the spinal canal. At 4.30 the anterior border of the IXth thoracic root-field ascertained.

"The upper edge of the lower field of reply runs from the mid-dorsal line about ·5 centim. below the lower edge of the isolated field. It runs at first almost horizontally, and then slopes downward more obliquely than the edge of the field above it. It passes below the scapula (arm horizontally extended) and reaches the ventral crosslap about 1·5 centims. below the point at which the lower edge in this isolated field reaches it, attaining the mid-ventral line about 6 centims. above the umbilicus of the individual."

IXth Thoracic.

Experiment.—*M. rhesus.* Female. 17.11.1890.

Measures 8·5 centims. from umbilicus to crest of pubes.

The Xth and XIth thoracic and the first three lumbar roots of the right side divided at 10.50. Final determination of posterior border of IXth thoracic skin field at 5.40.

"The lower edge of the upper field of reply starts from the mid-dorsal line about 1·2 centim. above the lowest point of the cage of the thorax, *i.e.*, tip of 12th rib. It passes over the last rib 1 centim. from its end, and about ·7 centim. above the lowest point of the cage of the thorax. Running almost horizontally for a couple of centimetres, it leaves the lateral aspect of the cage of the thorax between the tips of the 10th and 11th ribs. Up to this place, it has only descended slightly, that is to say, about 1·2 centim. from its level at the mid-dorsal line, but, from this point onwards, it slopes down rather more obliquely to reach the mid-ventral line 2·4 centims. above the umbilicus."

On *post-mortem* examination the pairs of ribs were ascertained to be twelve.

Xth Thoracic.

Experiment.—*M. rhesus.* Male, young. 24.11.1890. Plate 44, fig. 7.

Measurements:—

Pubes to infrasternal notch	17	centims.
Vertical distance from nipple to anterior superior spine .	14	„

At 9.10 the two lowest thoracic and the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, IXth, and Xth sub-thoracic roots of the right side severed. At 6.30 the posterior border of the Xth thoracic root finally ascertained.

"The lower edge of the upper field of reply runs obliquely downward and outward from the mid-dorsal line, passing about ·5 centim. below the point of the 12th rib, and keeping more horizontal from that point halfway to the mid-ventral line. It meets the mid-ventral line about 2 centims. above the umbilicus."

At autopsy the pairs of ribs were found to be twelve in number.

Xth Thoracic.

Experiment.—*M. rhesus.* Female; young. 17.12.1890.

Dimensions:—

Umbilicus to pubes	8·5	centims.
Nipple to pubes	21·5	„

At 11.30 the Vth, VIth, VIIIth and IXth thoracic roots of the right severed. The anterior border of the cutaneous field of the Xth thoracic root finally determined at 7.20.

"The upper limit of the lower field of reply is traceable by a line which may be followed from the mid-dorsal line about 7·5 centims. above the level of the umbilicus, and barely 5 centims. below the point at which the lower edge of the upper field of reply meets the mid-dorsal line" (*i.e.*, gap between IVth thoracic and Xth thoracic is barely 5 centims. wide). "The line, from that point, slopes downward and outwards," descending at an angle of about 75° with the long axis of the trunk. "Exhibiting but slight sinuosity, it slopes to the mid-ventral line, which it attains 4·5 centims. above the umbilicus, and 7 centims. below the point at which the lower edge of the upper field of reply attains it" (posterior border of IVth thoracic root field).

The number of ribs was found at the autopsy to be normal.

Xth Thoracic.

Experiment.—*M. rhesus.* Male. 15.10.1890.

Measurements:—

From top of symphysis to xiphoid is	17	centims.
From the tip of the 12th rib to the anterior superior spine	5·5	„

At 9·40 the XIth and XIIth thoracic and the Ist post-thoracic roots of the right side severed. At 6 P.M. the posterior border of the cutaneous field of the Xth thoracic finally determined.

"The lower edge of the upper field of reply starts from the mid-dorsal line on a level with the lowest part of the cage of the thorax, *i.e.*, nearly 6 centims. above the level of the anterior superior spinous process. It descends obliquely outward to the line of the transverse process, and from that line to 1·2 centim. below the tip of the 12th rib, and about 1 centim. below the lowest edge of the cage of the thorax, sweeps almost horizontally round the abdomen to 3 centims. from the mid-ventral line. At that distance from the mid-ventral line, it again descends more rapidly to reach the mid-ventral line about 1·2 centim. above the umbilicus, *i.e.*, about 10 centims. above the symphysis pubis."

Ribs and lumbar vertebræ normal in number.

XIth Thoracic.

Experiment.—*M. rhesus.* Female. 8.6.1891.

Measured:—

Middle of POUPART's ligament to nipple	19·5	centims.
„ „ „ „ inner head of tibia	10·5	„

The roots of the IXth and Xth thoracic nerves divided on the right side at 8.50 A.M. At 12.40 the anterior border of the XIth thoracic root-field determined.

"The upper edge of the lower field of reply starts from the mid-dorsal line about 1·5 centim. below the lower edge of the upper field of reply. It may be described as a line sloping downward slightly as it runs outward to about the mid-lateral line of the trunk. From that point it slopes more abruptly downward and reaches the ventral crossed overlap about 2 centims. above the umbilicus, about 2·5 centims. below the lower edge of the upper field of reply."

Ribs normal in number.

XIth Thoracic.

Experiment.—*M. rhesus.* Female; young. 10.10.1890.

Measurements:—

Anterior superior spine of ilium to tip of last rib	5·5	centims.
Umbilicus to crest of pubes	7·5	„

At 11 o'clock the XIIth thoracic and the Ist and IInd, the IVth, Vth, VIth, VIIth, and VIIIth post-thoracic roots of the right side severed. At 6 o'clock the posterior border of the cutaneous field of the XIth thoracic root finally determined.

"The lower boundary of the upper field of reply starts from the mid-dorsal line on a level about 1·5 centim. above the umbilical level. It descends thence in a curve, which is convex upward, to a point on a line 3 centims. from the mid-dorsal line, about 1 centim. below the level of the starting point. Running horizontally for the next 2 centims. it turns upward and comes to lie about 2·8 centims. below the apex of the 12th rib. Thence it sweeps downward gently so that 2 centims. from the mid-ventral line it is 1 centim. below the level of the umbilicus, and strikes the mid-ventral line 2·8 centims. below the umbilicus."

This is a higher position of the border than in the two other estimations of it, and may be due to individual variation, as the plexus on dissection was markedly post-fixed. But against that explanation, accounting for the entire discrepancy, is the fact that the field for the IIIrd lumbar root, which was determined in the same individual, did not differ much from the estimations in other individuals. It is probable that the full limits of the field of reply were curtailed by the depth of the anæsthesia and the exhaustion towards the end of the experiment.

Ribs, twelve in number each side.

XIIth Thoracic.

Experiment.—*M. rhesus.* Female; older. 12.11.1890.

Dimensions given p. 702.

At 11 o'clock the two highest and the IVth, Vth, VIth, VIIth, VIIIth, Xth, and XIth post-thoracic roots of the right side severed. At 6.50 the lower limit (posterior border) of the field of the XIIth thoracic root finally determined.

The lower limit of the upper field of reply is traced as a line starting from the mid-dorsal line

·8 centim. below the level of the umbilicus, about 3·5 centims. below the lowest point of the cage of the thorax. After sloping very slightly for the dorsal 3 centims. of its course, it turns more obliquely downward, presenting a slight convexity upward. It then curves inward toward the mid-ventral line, and meets that line at a point 4 centims. below the umbilicus. It is separated from the upper of the two isolated fields of reply (IIIrd lumbar) by about 1·5 centim. at the mid-dorsal line. At 3 centims. lateral from the mid-dorsal line the interval is only 1·1 centim., but near the mid-ventral line is greater, amounting where greatest to 4·5 centims."

XIIth Thoracic.

Experiment.—*M. rhesus.* Female. 17.11.90. Plate 45, fig. 8.

Measurements on p. 702.

The Xth and XIth thoracic, and the highest three lumbar roots of the right side divided at 10.50. Final determination of the isolated field of the XIIth thoracic at 6.30.

"The anterior edge of the isolated field of reply meets the mid-dorsal line 1 centim. behind the point at which the posterior edge of the upper field of reply (IXth thoracic) meets it. It passes just over the tip of the last rib, sloping downwards for a considerable distance, and then upward for a shorter distance, in order to do so. From the end of the last rib it runs downward and inward, descending somewhat more rapidly toward the mid-ventral line, which it reaches about ·8 centim. above the umbilicus."

"The posterior edge of the isolated skin field starts from the mid-dorsal line about on the horizontal level of the umbilicus, 3 centims. below the point at which the anterior edge meets the mid-dorsal line. Descending rather rapidly for the first 2·5 centims. of its outward course, it turns in a horizontal direction above the anterior superior iliac spine, at a distance of 1 centim. above it. It then descends again more rapidly, later less rapidly, to strike the mid-ventral line, 4·2 centims. below the umbilicus, *i.e.*, 4·5 centims. above the crest of the pubes."

"The dorsal border measures 3 centims. and laps across the mid-dorsal line for at least ·4 centim. The ventral border measures nearly 4 centims., and laps across the mid-ventral line by at least ·8 centim. in some places."

"The field appears narrowest at the dorsal border of it; widest a short distance from the ventral border of it."

At autopsy ribs ascertained to be twelve in number each side.

"The isolated field of reply (XIIth thoracic) is separated from the upper field (IXth thoracic) by a space of 1·2 centim. behind; by a space of more than 2 centims. near the mid-ventral line."

XIIth Thoracic.

Experiment.—*M. rhesus.* Female; young. 19.11.90. Plate 44, fig. 6.

The posterior roots of the Ist, IInd, IIIrd, Vth, VIth, VIIth, VIIIth, and IXth post-thoracic spinal nerves of the right side severed at 11.25. The lower (posterior) border of the skin field of the XIIth thoracic marked out at 3.30 finally.

"The border corresponds closely with that found for the XIIth dorsal, the last experiment. It slopes downward more steeply in front than behind. There seems a greater ventral crossed overlap than in the last experiment."

Ribs twelve in number each side.

XIth and XIIth Thoracic compared.

Experiment.—*M. rhesus.* Female. 7.1.91.

The posterior roots of the Ist and IInd, the IVth, Vth, VIth, VIIth, and VIIIth post-thoracic spinal roots of the right side divided at 11.40 A.M. At 1.50 the posterior root of the XIIth right thoracic also divided. Comparison of the posterior borders of the XIIth and XIth thoracic cutaneous fields.

"The two borders run fairly parallel, but slightly wider apart at the ventral crossed overlap. The distance between them certainly is not more than half the vertical depth of the XIIth thoracic field. Both reach the ventral crossed overlap below the umbilicus. It is clear that the umbilicus must lie about the middle of the XIth thoracic skin field. The ventral crossed overlap barely amounts to a centimetre in width."

Ribs twelve in number each side.

XIth and XIIth compared.

Experiment.—*M. rhesus.* Female. 12.11.1890. Plate 45, fig. 11.

The posterior borders of the XIth and XIIth thoracic were compared at end of experiment on the IIIrd post-thoracic, and similar results obtained to the result above.

Ist Post-thoracic.

Experiment.—*M. rhesus.* Male; young. 31.10.1890.

The measurements were—

From anterior superior spine to tendo patellæ . . .	18 centims.
,, xiphoid to pubes	16 ,,

At 9.50 A.M. the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, and IXth post-thoracic roots of the right side severed; at 3.30 the posterior border of the cutaneous field of the Ist lumbar finally determined.

"The lower edge of the upper field of reply starts from the mid-dorsal line, about 3·5 centims. above the level of the highest point of the iliac crest, or probably just below the lower edge of the spinous process of the 3rd vertebra, in front of the sacrum (Vth lumbar). It slants outward from the mid-dorsal line, and, on reaching the line of the tips of the transverse processes, it curves downward more obliquely to the anterior superior angle of the crista ilii (reaching the level of the crista just medial to the anterior superior spine. It sweeps forward and downward to the inguinal fold, and then turns a little way down the thigh, and stops to pass inward, parallel and above the inguinal fold across toward the horizontal limb of the pubes, which it reaches about over the medial edge of the obturator foramen. On the pubes it approaches the isolated field of reply, but it is doubtful whether they really join" (Ist lumbar and Vth lumbar).

Ist Post-thoracic.

Experiment.—*M. rhesus.* Male; young. 24.11.1890. Plate 44, fig. 7.

Measured—

Pubes to infrasternal notch	17 centims.
Anterior superior spine to nipple	14 ,,

At 9 the two lowest thoracic roots and the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, IXth, and Xth spinal roots of the right side divided. At 6·5 the skin field of the Ist lumbar finally delimited.

"The anterior edge of the upper of the isolated skin field of reply slants outward and slightly downward from the mid-dorsal line to a point 2·7 centims. below the tip of the last rib, on a line from the tip of the last rib to the anterior superior iliac spine, the length of the line being 6·5 centims. The line then slopes more rapidly downward, and strikes the mid-ventral line about 1 centim. below the umbilicus."

"The posterior edge of this isolated field of reply runs from the mid-dorsum, at a point just anterior to the level of the anterior superior iliac spine, and along a line close above the iliac crest. It meets the iliac crest about 1 centim. behind the anterior superior spine, passes 1 centim. below that spine, and curves downward and ventralward to a few millimetres below the spine of the pubes; on the rectus abdominis fold it descends a short way, and returns upwards on itself. About midway between the anterior superior spine of the ilium and the spine of the pubes the line descends, making a convex sweep downward, so as to form a shallow tongue pointed towards the knee."

The number of ribs was twelve pairs.

"The dorsal border measures 8·5 centims. The ventral border measures nearly 8 centims. The greatest vertical depth of the field is 8·5 centims."

Ist Post-thoracic.

Experiment.—*M. rhesus.* Female. 20.2.1891.

Dimensions, see Experiment.

At 10.50 the posterior roots of the IInd, IIIrd, IVth, Vth, VIIth, and VIIIth post-thoracic nerves of the right side divided. At 4 o'clock the final estimation of the field belonging to the posterior border of the Ist post-thoracic completely found.

"The lower edge of the upper field of reply passes from a point near the mid-ventral line, on the front of the pubes, and ascends, passing outwards along the fold of the groin, thrusting a little projection downward on the top of SCARPA's triangle. It reaches a point in the line of the anterior superior iliac spine about ·5 centim. below it, and then runs backward more horizontally to reach the mid-dorsal line, somewhat above the level of the anterior superior spine."

Ist Post-thoracic.

Experiment.—*M. rhesus.* Female. 22.12.1890.

Measured :—

Umbilicus to pubes	8 centims.
Anterior superior spine of ilium to nipple	7·5 „

At 9.40 the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, IXth, and Xth spinal roots of the right side divided intraspinally. At 2.5 the posterior border of the field of cutaneous distribution of the Ist lumbar finally delimited.

"The lower edge of the upper field of reply runs from the mid-dorsal line at a level about 1 centim. higher than that of the anterior superior spine of the ilium. It slopes downwards and forwards, passing over the anterior superior spine about ·4 centim. above it. It slopes downward above, but parallel with the inguinal fold. It meets the mid-ventral line decidedly lower than mid-way between the pubes and the umbilicus." "There is a slight spur from this upper field pushed out toward the limb in front of the anterior superior spinous process of the ilium."

Twelve ribs each side.

IInd Post-thoracic.

Experiment.—*M. rhesus.* Male. 27.10.1890.

Measurements :—

Top of symphysis to xiphoid	17 centims.
Tip of 12th rib to anterior superior spine	5·5 „

At 9.40 the two lowest thoracic and the Ist lumbar and the IIIrd, IVth, Vth, and VIth lumbar roots of the right side severed. At 7.30 the limits of the field of cutaneous distribution of the IInd lumbar root ascertained finally.

"The upper edge of the isolated field of reply stretches from the mid-dorsal line 3 centims. in front of the level of the crista ilii, and descends to 2 centims. above the level of the crest in the line of the anterior superior spinous process. From that position it slopes downward and inward at some distance above the inguinal fold with a slightly sinuous course to a point on the mid-ventral line, just higher than midway between the top of the symphysis pubis and the umbilical scar."

"The lower edge of the isolated field of reply stretches from the mid-dorsal line at a point about 1·5 centim. below the level of the anterior superior spinous process of the ilium, and then slopes, at first less, later more steeply outwards and downward, so that it crosses the vertical dropped from the anterior superior spinous process about 4·2 centims. below the spinous process. It follows a course down the sartorio-rectus fold, gradually turning over the crest of that toward the anterior aspect of the thigh, and descends the thigh as low as the apex of SCARPA's triangle, but rather to the outer side of that. It then recurves on its course, enclosing a tongue-shaped flap, and sweeps inward and upward to the middle of the front of the symphysis."

"The shape of the isolated field of reply may be described as broadly strap-shaped, the wider end of the strap lying on the thigh."

IInd Post-thoracic.

Experiment.—*M. rhesus.* Female. 13.2.1891.

The IIIrd, IVth, Vth, VIIth, and VIIIth post-thoracic roots of the right side cut at 11.20. At 1.45 the lower edge of the upper field of reply, *i.e.*, the posterior border of the IInd lumbar, was determined.

"The lower edge of the upper field of reply starts from near the mid-ventral line at the front of the pubes, and curves down the thigh on the extensor mass to about half-way between POUPART's ligament and the knee. It turns upward then and runs above the hip to about 3 centims. below the anterior superior spinous process of the ilium, and reaches the mid-dorsal line somewhat higher, about 2 centims. in front of the anterior border of the gluteal field of reply."

Ribs, the normal twelve on each side.

Ist and IInd Post-thoracic compared.

Experiment.—*M. rhesus.* Male. 3.11.1890.

Measurements:—See p. 726.

The posterior border of the cutaneous field of the Ist lumbar compared with that of the IInd lumbar.

At 9.40 the IIIrd and IVth, the VIth, VIIth, VIIIth, and IXth post-thoracic roots of the right side severed. The posterior border of the IInd lumbar was delimited at 12.30, and then the IInd lumbar root was severed, and at 4.50 the posterior border of the cutaneous field of the Ist lumbar was finally determined.

"The lower border of the upper field of reply runs from a point in the mid-dorsal line about 3 centims. below the level of the anterior superior spinous process of the ilium outward about ·8 centim. above the inner angle of the iliac crest, crossing over the crest about 1·2 centim. ventral to the inner angle, and meeting the outer edge of the crest about 1·5 centim. below the anterior superior spine. Thence descending along the crest of the sartorio-rectus fold to 1 centim. below the level of the line from the top of the great trochanter to the top of the symphysis. It curves from that point inwards, and then retreats upwards before again descending. It meets the isolated field of reply" (Vth lumbar) "and then, separating from it again, attains the mid-ventral line on the symphysis pubis." "The place at which it appears to meet the isolated field of reply is about 1 centim. to the median side of the apex of SCARPA's triangle."

"The lower edge of the upper field of reply has retreated to a various extent at various portions of it. It now represents a nerve-root one segment higher than that which it did previously. The limit now runs from the mid-line of the back 1·5 centim. higher than it did before, *i.e.*, about 1·5 centim. below the level of the anterior superior spinous process. It slants in an outward direction as before, but more nearly horizontally now, until about 3 centims. distant from the mid-dorsal line, when it turns downward obliquely to pass about 1 centim. or less behind and below the anterior superior spine of the ilium, and sweeps forward following the line of the posterior border of the previous limit" (IInd lumbar), "but about 15 millims. above it. It keeps parallel to the previous line for a short distance, and then turns downward and inward, with a shallow projection convex towards the thigh, along but soon above the inguinal fold. About 1 centim. above the root of the penis it passes on to the front of the pubes."

IInd Post-thoracic.

Experiment.—*M. rhesus.* Male. 19.10.1890.

Measurements not taken.

At 10.10 the IIIrd, IVth, Vth, VIIth, and VIIIth roots of the right post-thoracic nerves divided in the spinal canal: at 4.20 the posterior border of the cutaneous field of the IInd lumbar ascertained.

"The lower edge of the upper field of reply may be traced by a line starting from a point near the mid-venter above the root of the penis, thence following roughly the inner horizontal half of POUPART's ligament and then almost suddenly descending the thigh on SCARPA's triangle, tending outward gradually toward the crest of the extensor mass rather more than halfway down the thigh. From that, its lowest level, it turns upward on the rectus and sartorius to run about ·6 centim. below the anterior superior spine, and thence inclines gradually upwards and inwards until it meets the mid-dorsal line."

Twelve ribs on each side.

IIIrd Post-thoracic.

Experiment.—*M. rhesus.* Female; young. 19.5.1891.

Dimensions not measured.

At 10.15 the IVth, Vth, VIth, VIIth, VIIIth, IXth, and XIth and XIIth post-thoracic roots severed on the right side. At 5.20 the upper field of reply delimited below (found to consist entirely of the posterior border of the IIIrd lumbar).

"The lower edge of the upper field of reply is traced from the mid-dorsum at a level 4 centims. below the level of the anterior superior spine of the ilium, and slopes downward and outward to enter the external aspect of the thigh about 5·5 centims. below the anterior superior spine of the ilium. It descends the thigh, encroaching more and more on the anterior aspect as it does so, and about 1·5 centims. above the upper border of the patella turns inward, still sloping so as to nearly reach the inner angle of the upper border of the patella. It then sweeps inwards, and increasing in steepness ascends the inner side of the anterior aspect of the thigh on the anterior border of the adductor fold, and finally reaches the front of the pubes near the lower edge of the symphysis."

Whether this edge is entirely composed of the field of the IIIrd lumbar or not will be discussed later.

Twelve pairs of ribs.

IIIrd Post-thoracic.

Experiment.—*M. rhesus.* Female; older. 12.11.1890. Plate 45, fig. 11.

Dimensions measured were—

Anterior superior spine to patella . .	17·5	centims.
" " " ankle . .	30	"
Pubes to umbilicus	9	"

The two highest and the IVth, Vth, VIth, VIIth, VIIIth, Xth, and XIth post-thoracic roots of the right side severed at 11 o'clock. At 6 o'clock the upper of the two isolated skin fields (that of the IIIrd lumbar root) finally delimited.

"The anterior edge (upper edge) of the isolated field of reply has been traced from the mid-dorsal line at a point 2 centims. in front of a line joining the highest points of the crests of the right and left ilia. Sloping steeply down at first it soon afterwards curves more outward, and at a point 4 centims. from the mid-line is running almost horizontally at a distance of 5·5 centims. below the tip of the last rib. Thence it turns steeply downward again to a point about 1 centim. anterior to the anterior superior spine, whence it again descends, giving a figure curved convexly upward to reach POUPART's ligament just inside the middle point of the ligament. It follows the line of the inguinal fold to the spine of the pubes, reaching the mid-ventral line 3 centims. above the ventral end of the posterior border of the field."

"The lower edge of this field of reply starts from the mid-dorsal line about 2 centims. below (posterior to) the upper edge, and about 1·6 centim. in front of the anterior edge of the lower isolated field of reply (IXth post-thoracic). It runs outward and downward parallel to the anterior edge of the lower isolated field (IXth post-thoracic) to a point about ·4 centim. above the top of the great trochanter. Thence the line descends less steeply over the external anterior aspect of the thigh to about 1 centim. above the patella; it reaches its lowest point somewhat less than 1 centim. internal to the inner edge of the quadriceps extensor tendon above the patella. It then ascends on the intero-anterior aspect of the thigh, passing over the fold marking the prominent edge of the adductor group at the junction of the lowest and middle thirds of the thigh. It runs parallel to the pubic fold, but ·8 centim. anterior to the crest of that fold, and reaches the mid-ventral line ·5 centim. above the junction of the right and left pubic folds."

Twelve ribs on each side.

IIIrd Post-thoracic.

Experiment.—*M. rhesus.* Female. 25.10.1890.

Measurements not taken.

The posterior divisions of the IVth, Vth, VIIth, VIIIth, and IXth post-thoracic spinal nerves of the right side divided in the vertebral canal at 11.15. At 7.25 the field of cutaneous distribution of the IIIrd lumbar (its posterior boundary) was examined finally. The examination confirmed previous ones, but did not give a field that tallied with observations on other individuals.

"The posterior edge of the upper field of reply lies about 1 centim. above the anterior edge of the lower field. It passes down the outer side of the thigh and then turns inward across the front of the thigh at a level rather above half-way between groin and knee; it soon ascends again, forming a narrow peak on the front of the thigh and sloping then less obliquely upwards, reaches the inner edge of the thigh close to the genital fold."

This lower limit for the field of the IIIrd lumbar is unusually low; it does not appear an error of experiment, because it was found later that the areas of the VIth and Xth post-thoracic nerves were all of them displaced in a similar sense in this experiment, and subsequent dissection revealed a very post-fixed lumbo-sacral plexus. The ribs and lumbar vertebræ were counted carefully and there was no abnormality in their number.

IIIrd Post-thoracic.

Experiment.—*M. rhesus.* Female; young. 10.11.1890.

Measurements not taken.

At 11 A.M. the lowest thoracic and the two highest lumbar, and the IVth, Vth, VIth, VIIth, and VIIIth post-thoracic roots of the right side severed. At 5.5 the area of cutaneous distribution of the [illegible]

"The upper border of the isolated field of reply starts from the mid-dorsum 3·5 centims. in front of the point at which the lower border of the field meets the mid-dorsum, and about 2 centims. above a line joining the highest points of the crests of the right and left ilia. Sloping steeply down at first it soon curves more outward, and at a point 4 centims. from the mid-dorsum runs almost horizontally at a distance of 5·5 centims. below the tip of the last rib. Thence it slopes steeply downward again to a point 1 centim. anterior to the anterior superior spine of the ilium, whence it descends with a border convexly curved upward to each POUPART'S ligament just inside its middle point. It follows the inguinal fold to the spine of the pubes, reaching the mid-ventral line 3 centims. above the ventral extremity of the posterior border of the field."

"The posterior border starts from the mid-dorsal line 1·6 centim. in front of the anterior border of the posterior field of reply." (Root IXth post-thoracic.) "It passes downward and outward parallel to that border to a point ·3 centim. above the top of the great trochanter. Thence the limit descends less steeply over the extero-anterior aspect of the thigh to 1 centim. above the patella; it reaches, however, its lowest point somewhat less than 1 centim. above the inner border of the quadriceps extensor tendon above the patella. It then ascends on the internal anterior aspect of the thigh passing over the fold marking the edge of the adductor group, and about the level of junction of the middle third with the lowest third of the thigh. It runs parallel with the pubic fold, but about ·8 centim. anterior to the crest of that fold, and reaches the mid-ventral line ·5 centim. anterior to the junction of the right and left pubic folds.

"The dorsal border is 3·5 centims. long and laps at least ·4 centim. across the mid-dorsal line." As to the size and position of that portion of the edge of the field that must be considered the ventral border, later considerations will be urged to settle that point.

The ribs are twelve in number.

IVth Post-thoracic.

Experiment.—*M. rhesus.* Female; small. 17.11.1890. Plate 44, fig. 8.

Measurements, on p. 702.

The Xth and XIth thoracic and the highest three lumbar roots of the right side severed at 10.50. Final determination of the anterior border of the IVth lumbar root at 7.10.

"The anterior edge of the lower field of reply starts from the mid-dorsal line ·2 centim. above the level of the crest of the ilium, descends to that crest, meeting it 1·2 centim. dorsal to the anterior superior spinous process; it crosses to 1 centim. below the anterior superior spine, running close below POUPART'S ligament in its outer half, and turns down the limb just on the crest of the prominence of the rectus femoris; it follows that direction to as far as a point rather more than 3 centims. below the inguinal flexure, and then turning inwards soon doubles back across SCARPA'S triangle to 1·4 centim. below POUPART'S ligament. Then again it sweeps inward, and running for a short distance almost horizontally, approaches the mid-ventral line, not, however, to reach it, for turning downward about 1 centim. away from the mid-ventral line it strikes the genital fold 1·5 centim. from the angle of the notch."

Ribs twelve in number each side.

IVth Post-thoracic.

Experiment.—*M. rhesus.* Female; young. 19.11.1890. Plate 44, fig. 6.

Measures—

From anterior superior iliac spine to spine of pubes . .	10·5	centims.
,, ,, ,, ,, tip of 3rd digit . .	38	,,

At 12.15 the posterior divisions of the Xth and XIth thoracic, and the highest three lumbar, and the

Vth, VIth, VIIth, VIIIth, and IXth post-thoracic roots of the right side severed. At 4.30 the area of distribution of the IVth lumbar root determined finally.

"The isolated field of reply is a broad flag-shaped band extending ventrally from a relatively narrow attachment to the mid-dorsal line. The upper border of the field is deeply notched; the lower border passes below the knee obliquely. The limit of the area may be traced thus from the mid-dorsal line. Starting at a point in the mid-dorsal line distinctly below the level of the level of the umbilicus, it runs outwards from the middle with a gradually increasing downward slope to a point about 1 centim. below the anterior superior spine of the iliac crest, and then follows the fold caused by the rectus muscle and sartorious, somewhat to the medial side of that fold into the front of the thigh. Thence it returns on itself towards POUPART's ligament for about 2 centims., and then once more curves inward and downward, lying on the front of the pubes but a full centimetre from the mid-ventral line. It then courses down the inner border of the thigh and leg behind the anterior edge of the gracilis fold, and over the medial belly of the gastrocnemius to reach the junction of the middle and lowest thirds of the leg on the postero-internal aspect of the leg; in this specimen 3 centims. above the point of the heel. Thence the line sweeps boldly round and forward, and turns upward obliquely over the skin, passing about 2·5 centims. below the patellar tendon and over the head of the fibula to reach the outer aspect of the thigh and slope across its anterior half, reaching the middle of the outer aspect about halfway up the thigh. It then ascends in a direction parallel with the long axis of the limb, and crosses a vertical dropped from the anterior superior spine about 7 centims. below that spine; finally it runs, ascending less sharply, to the mid-dorsal line, which it reaches 5 centims. below the point at which the anterior border of the field reaches it."

"The circumference of the thigh in its upper third being 15 centims., just about 7½ (one-half) is supplied by this root field, and that half reaches from the middle of the outer aspect of the thigh to the inner edge of the thigh."

At the autopsy it was ascertained that the number of ribs and lumbar vertebræ was normal.

Photograph. Plate 44, fig. 6.

IVth and IIIrd Post-thoracic compared.

Experiment.—*M. rhesus.* Female. 26.9.1890.

Measurements not taken.

The posterior roots of the Vth, VIth, VIIth, IXth, and Xth post-thoracic nerves of the right side divided in the spinal canal at 9.10 A.M. Later the IVth post-thoracic root divided. Portion of the lower edge of the IVth lumbar, later the lower edge of the IIIrd lumbar examined.

"The anterior peak of the field of reply" (this peak is IVth lumbar) "descends over the front of the knee. It is bounded by a line that passes from a point on the outer aspect of the knee downwards and forwards over the crest of the tibia to the inner side of the skin, and then ascends on the inner face of the knee along the gracilis fold to a point about halfway up the inner border of the thigh."

After the last section:

"The lower edge of the upper field of reply starts from the mid-dorsal line above the root of the tail, and descends the outer side of the thigh over the hip gradually, in the lower half of the thigh, sloping inward over the extensor mass of the thigh to cross the front of the thigh above the patella and then turns upwards and inwards, meeting the inner edge of the thigh below the inguinal fold, and the outer border of the 'genital flap.'"

Vth Post-thoracic.

Experiment.—*M. rhesus.* Male; young. 29.10.1890.

Measurements, *vide supra.*

[illegible] VIth, VIIth, VIIIth, IXth, XIth, and XIIth post-thoracic roots of the right side severed. At 8 o'clock the posterior border of the combined fields of the IIIrd, IVth, and Vth post-thoracic roots delimited.

"The posterior edge of the upper field of reply starts from the mid-dorsal line about 4 centims. below the level of the crest of the ilium; turning downwards and outwards the line sweeps along the middle of the outer aspect of the thigh to behind and above the head of the fibula, and then follows the leg down to pass over the front of the ankle and on the dorsum pedis reach the space between the 2nd and 3rd metatarsal bones; it runs along the 2nd digit, recurves on the medial aspect of the terminal joint, reaches the web between hallux and 2nd digit, and courses along the middle of the prominence caused by the plantar muscles of the hallux, to ascend finally in the groove between the heel and the internal malleolus. It sweeps up the inner aspect of the leg over the inner head of the gastrocnemius, and then accurately along the internal *border* of the thigh and the genital crest and notch to the pubes."

The portions of this boundary which belong respectively to the IIIrd, IVth, and Vth roots will be discussed later; the portion belonging to the IIIrd is quite small.

Vth Post-thoracic.

Experiment.—*M. rhesus.* Male; young. 24.11.1890. Plate 44, fig. 7.

The two lowest thoracic nerve-roots and the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, IXth, and Xth post-thoracic roots of the right side severed at 9.10.

The isolated area of the Vth lumbar delimited at 5.20.

"The edge of the isolated field of reply passes from a point 1 centim. from the mid-ventral line, halfway between the top of the symphysis pubis and the root of the penis downward and outward, sloping across the inner aspect of the thigh to the mid-quadriceps line, which it crosses above the top of the patella about 1 centim. above the patella, and then retires up the thigh again for about 2 centims. to gain the outer aspect of the thigh, and descend along the middle of it and the middle of the outer aspect of the knee over the peroneal group of muscles to the groove in front of the external malleolus; it enters the dorsum of the foot close to the outer side of the head of the astragalus, and somewhat distal to the tarso-metatarsal joint sweeps inwards, bisecting the first interdigital web. It curves round the hallux along the extreme limits of the aspect of the phalanges of the hallux, encroaching somewhat on the plantar surface along the inner edge, and passing distinctly on the plantar face of the foot about 1 centim. from the inner edge. It leaves the sole of the foot midway between calcaneum and internal malleolus to ascend on the inner edge of the tendo Achillis for 3 centims. before turning backward, always ascending, over the inner belly of the gastrocnemius to reach the fold of the inner hamstrings. The crest of that fold it gradually crosses, appearing on the prominence of the inner hamstring group at the postero-external aspect, about 2 centims. behind the scrotal flexure. It turns backward and inward so as to cross that fold again, and just in front of it, or on it, meets the point whence it started about 1 centim. from the ventral median line."

At the autopsy the ribs were found to be twelve in number.

Vth Post-thoracic.

Experiment.—*M. rhesus.* Male; young. 31.10.1890. Plate 46, fig. 12.

Measurement, *vide supra.*

The IInd, IIIrd, IVth, VIth, VIIth, VIIIth, and IXth post-thoracic roots of the right side severed at 9.50 A.M. The field of cutaneous distribution of the Vth lumbar explored and finally settled at 4.15 P.M.

"The edge of the isolated field of reply lies midway between the internal malleolus and the point of the heel; thence it passes along the sole of the foot along the line of the bones of the hallux, and upon the under surface of the hallux, tending toward its inner aspect, and, curving round the point of it, passes to the edge of the web between hallux and 2nd digit. After reaching the inner side of the dorsal aspect of the proximal joint of that digit, it runs up the middle of the dorsum of the foot to the front of the ankle, and ascends the leg. About one-third up the leg it sweeps round to the outer aspect of the leg, reaches the external head of the gastrocnemius, and passes behind the head of the fibula to the middle of the outer aspect of the thigh. It then returns across the front of the thigh, showing a notch at least 3 centims. deep on the rectus fold, and sweeps obliquely inwards to the front of the pubes, which it barely reaches, before it re-curves, and descends a little behind the actual inner edge of the thigh to the crest of the inner hamstring and inner head of the gastrocnemius, and running down the groove internal to the tendo Achillis, reaches again the hind part between the heel and the internal malleolus."

Ribs twelve in number on each side.

Vth Post-thoracic.

Experiment.—*M. rhesus*. Female; young. 22.12.1890.

At 9.40 A.M. the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, IXth, and Xth post-thoracic roots severed.

At 4.15 the Vth post-thoracic field delimited finally.

"Starting from the outer edge of the nail of the hallux, it ascends along the lateral edge of the dorsal aspect of the hallux, the limiting line runs up the first intermetatarsal space near to the side of the first metatarsal bone, sweeping round the lateral edge of the first tarso-metatarsal joint, and then turning inward so as to strike the fold over the tibialis anticus tendon just distal to the astragalo-cuneiform joint. The line follows the tibialis anticus tendon upward, and at same time tends somewhat outward as well as upward, lying a little nearer the inner than the outer malleolus, and obliquely rising to cross the tibialis-peroneal septum three-quarters of an inch below the halfway point between knee and ankle. The line meets the outer edge of the gastrocnemius a little above that halfway point. It lies as far behind the head of the fibula as that head lies behind the anterior edge of the limb, and at level of point of knee lies at the junction of the third, and the most posterior quarter of the outer aspect. The distance from the great trochanter to the outer condyle being 10·5 centims., the limit of the area rises 4·5 centims. below the great trochanter, reaching that, its highest point, a little in front of the middle of the outer aspect of the thigh. Thence the line doubles back about 1 centim. behind the anterior border of the thigh to within 1·5 centim. of the patella, outer side. It then returns and crosses the mid-line of the anterior aspect of the thigh 3·5 centims. above the top of the patella. It crosses the inner sartorius fold 4·5 centims. below the middle point of POUPART'S ligament. Having reached its highest point just in front of the inner edge of the thigh, the line crosses the genital fold 1·5 centim. below the genital notch, and then immediately descends along the crest of the fold caused by the inner hamstring, and for 2·5 centims. down the protrusion over the inner head of the gastrocnemius to sweep on to inner aspect of leg, passing, as it does so, midway between the inner malleolus and the crest of the tendo Achillis ridge. It passes along the line of the tendon of the tibialis anticus, and onwards to the inner side of the sole just, but not far, on the hallucial prominence to the inner side of the proximal phalanx of the thumb. It there gains the point whence it was traced in this description, and reaches it by such a path as to include the medial, but not the lateral, part of the plantar aspect of the hallux."

"The circumference of the knee in the extended position of the limb being 14 centims., the Vth lumbar field occupies 10·5 centims. of the circumference. The shape of the area is, roughly speaking, a very elongated ace of hearts, the base of the heart turned toward the inguinal fold, and the notch in the base lying on the front of the thigh."

Ribs twelve in number on either side.

Vth Post-thoracic.

Experiment.—*M. rhesus.* Male. 29.12.1890.

Measured:—

Pubes to infrasternal notch	17 centims.
Vertical distance from nipple to anterior superior spine .	14 ,,

At 9 A.M. the Xth, XIth, and XIIth thoracic, the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, IXth, and Xth post-thoracic roots divided intraspinally.

At 5.30 the isolated field of reply examined for the last time.

"The field is roughly triangular with its base upon the thigh, its acutest angle at the apex of the hallux. It is limited by a line which has been made out along the inner edge of the thigh at the junction of the inner and posterior aspects of the limb. It descends thence along the leg, over inner head of gastrocnemius to groove behind internal malleolus. It runs over the plantar surface to the hallux, and turns over the web between hallux and the 2nd digit, to run along the dorsum (where the boundary is not easily determined) to the outer side of the front of the ankle-joint, close in front of the external malleolus. It ascends on the prominence caused by the peroneal group, and behind the head of the fibula and biceps tendon, then coming forward higher up and turning, obliquely ascending, over the extensor mass of the thigh. The line above the knee runs down a little toward the knee, then again pursues its oblique ascending course, and crosses the adductor group to attain the inner border of the thigh about half-way between hip and knee."

Vth Post-thoracic.

Experiment.—*M. rhesus.* Male. 3.11.1890.

Measurements:—

Symphysis to umbilicus	8·5 centims.
Anterior superior spine of ilium to ligamentum patellæ .	18 ,,

The field of cutaneous distribution of the Vth lumbar root.

At 9.45 the IIIrd, IVth, VIth, VIIth, VIIIth, and IXth post-thoracic roots of the right side severed; later; the IInd also.

At 4.20 the cutaneous field of the Vth finally examined.

"The isolated area of reflex response is limited by a line that may be traced as follows:—Starting behind the head of the fibula, it descends the leg, and passes at about the mid-point of the anterior aspect of the ankle-joint on to the dorsum pedis; it reaches the inner side of the 2nd digit, curves round the root of that and runs up the inner part of the plantar surface to the inner face of the heel, ascends to the shin over the inner head of the gastrocnemius, thence along the inner edge of the thigh, nearly to the front of the pubes, but recurves before actually reaching that point. It then sweeps with a convexity upward, toward the knee on the extensor group of the thigh, and, leaving a bold notch, returns again toward the trunk on the outer aspect of the thigh, but does not retire beyond half-way up the thigh. Descending the outer face of the thigh toward the knee again, it passes to the point behind the fibular head from which it was originally traced."

Ribs, twelve on each side.

VIth Post-thoracic.

Experiment.—*M. rhesus.* Male. 27.1.1891. Plate 45, figs. 9 and 10.

Measurements not taken.

At 12.25 the posterior divisions of the Ist, IInd, IIIrd, IVth, Vth, VIIth, VIIIth, and IXth post-thoracic spinal nerves of the right side severed intraspinally.

Delimitation of the cutaneous field of the VIth post-thoracic root, at 7.40 P.M. completed.

"The isolated field of reply is an area completely detached from the mid-dorsal line and from the mid-ventral line. It occupies solely the skin of the limb proper. Its border is traceable by a line as follows. It lies 1 centim. to the outer side of the tendo patellæ, and from that spot descends, tending gradually toward the crest of the shin, and crossing inwards over that crest at a little below the junction of the middle and lowest thirds of the leg. It descends to within 2·5 centims. of the ankle-joint, and then returns upward sloping over the inner face of the shin to pass upward behind the fold of the gracilis. Just above the knee-joint it turns slantingly backwards over the inner hamstrings to about half-way up the posterior aspect of the thigh, passes almost in a straight line across to the outer (lateral) aspect of the thigh. This lateral aspect it turns across to a point about midway between the anterior and posterior borders of it, so that it reaches a point slightly above the mid-point of the lateral aspect of the thigh. At this point it turns abruptly at almost a right angle to descend the thigh near the external margin of the rectus femoris, and finally attains the outer side of the patella, and the point whence it was traced."

Normal number of ribs present on each side.

VIth Post-thoracic.

Experiment.—*M. rhesus.* Male. 19.10.1890.

Measurements not taken.

Delimitation of cutaneous field of VIth lumbar.

At 10.10 the IIIrd, IVth, Vth, VIIth, and VIIIth roots of the right post-thoracic nerves divided in the spinal canal.

At 4.50 the area of the isolated field of response completely delimited.

"The isolated field of reply is limited by a line traceable as follows:—Starting from the front of the shin bone, about one-third up the leg, it turns in an ascending direction obliquely inward to the edge of the calf muscles, and, along the inner edge of the gastrocnemius, follows behind the fold of the gracilis to run up above the ham to about the level at which the inner and outer hamstring groups converge at the top of the popliteal space. Having passed a little above and external to that point, the border suddenly retreats down the limb again, descending upon the head of the fibula to sweep above the peroneal group and reaches the anterior tibial group, and so gains the crest of the tibia and the point whence it was traced."

"On the outer edge of the foot, from the external malleolus to the base of the 5th digit, a small oval patch of extremely dull response exists; so dull that, in the earlier determinations, I questioned whether response was obtainable at all, and marked it provisionally as not giving reply. In the final delimitation, this area did seem to give a feeble response (extension of ankle), and I am not, therefore, clear about it."

The above line marked the upper boundary of the field of reply which included the whole of the distal end of the limb.

Normal number of ribs on each side.

VIth Post-thoracic.

Experiment.—*M. rhesus.* Female. 25.10.1890.

Delimitation of field of VIth lumbar nerve.

At 11.15 the IVth, Vth, VIIth, VIIIth, and IXth post-thoracic roots of the right side divided in the spinal canal. At 9.10 the field of cutaneous distribution of the VIth post-thoracic finally delimited.

"This field does not agree with the field delimited on the 20th in some points, but bears a strong [illegible] that it is limited by a line which may be followed from the skin over the [illegible] above the heel, and turns downward under the external malleolus to recurve upward along the peroneal group, soon bending backward, and lying on the outer head of the gastrocnemius. The line follows the middle of the popliteal space to reach the outer hamstring above that space, and, on the outer aspect of the thigh, turns down over the head of the fibula to reach the crest of the shin about 4 centims. below the patella, and slope over the inner aspect of the leg to the lower third of the leg, whence it returns again upwards between the inner malleolus and the tendo Achillis to reach the point it was traced from, about 5 centims. above the heel."

Ribs and lumbar vertebræ normal in number. Lumbar plexus markedly post-fixed.

VIth Post-thoracic.

Experiment.—*M. rhesus.* Female. 13.2.1891.

The IIIrd, IVth, Vth, VIIth, and VIIIth post-thoracic roots of the right side severed at 11.20. At 2 o'clock the field of cutaneous distribution of the VIth lumbar to touch was satisfactorily marked out. At 2.10 the rootlets composing the posterior half of the root were divided, and at 3.50 the cutaneous field of the reduced root again delimited, and finished at 4.15.

"The isolated field of reply occupies the distal extremity of the limb, and agrees closely with the area found in previous experiments to be that of the VIth post-thoracic. It is bounded by a line that can be traced from close above the internal malleolus upwards along the inner face of the tibial shaft and the inner condyle to the inner hamstring, the top of the popliteal space, and finally the biceps mass about half way up it. From that position, on the outer aspect of the thigh, it returns abruptly down the thigh, crosses the shin about 2 centims. below the tubercle of the tibia, and, running obliquely over the subcutaneous face of the tibia, gains the position whence it was traced."

At 2.10 the posterior half of the posterior root was cut through. The cutaneous field of reflex response was soon after roughly examined, but no distinct change in it detected. At 3.50 it was carefully examined in every part. "I cannot detect that the field is sensibly diminished in size. The only difference that is certain is a diminution, but not abolition, of the reflex response from the top of the ham, and to a less extent along the prominence of the calf." It was found the posterior half of the posterior root had really been severed, as supposed.

VIth Post-thoracic.

Experiment.—*M. rhesus.* Female. 20.2.1891. Plate 46, fig. 13.

At 10.50 the IInd, IIIrd, IVth, Vth, VIIth, and VIIIth roots of the post-thoracic nerves of the right side divided. At 4.30 the final estimation of the field belonging to the VIth lumbar root. The rootlets composing the posterior half of the root then severed. The cutaneous field of the anterior half of the nerve-root then compared with the previously delimited field one hour after the 2nd section.

"The isolated field of reply occupies the distal extremity of the limb, and is bounded by a line that is traceable as follows:—Commencing from a point about half way up the outer aspect of the thigh, and midway between its anterior and posterior borders, it runs down the thigh almost directly to reach the front of the head of the fibula. Continuing this oblique course downwards and inwards, it surmounts the crest of the tibia about the junction of the upper and middle thirds of that bone, and slants over the shin to a point about 3 centims. above the lower articular end of the bone. The line then abruptly ascends the inner aspect of the leg, passes along the back of the gracilis not far above the knee, sweeps obliquely upward and backward over the upper apex of the popliteal space, and finally over the edge of the outer hamstring to the point whence it was at first followed."

At 4.40 the lower half of the posterior root was severed. "At 5.45 the field was finally delimited in its present condition. No change was detected in the extent of the field in any direction except the following:—It was found that the boundary where it lies above the popliteal space, and especially on the outer hamstring, had retreated downward toward the knee. The amount of retreat is at most somewhat more than 1 centim. The reply to touch from the whole of the foot seems even more brisk than before, when the whole root was intact, but the skin on the summit of the calf seems to reply less briskly than before. Elsewhere no detectable difference appears at all.

Number of ribs and lumbar vertebræ normal.

VIth Post-thoracic.

Experiment.—*M. rhesus.* Female. 16.3.1891.

At 11.20 the IIIrd, IVth, Vth, VIIth, VIIIth and IXth post-thoracic spinal nerves (posterior roots only) of the right side divided. The isolated field of the VIth delimited finally at 4.45.

"The field of reply is evidently that of the VIth lumbar, and it corresponds so closely with the field found on the 13th and 20th of last month, there is no need for again describing it. There is distinct response from the whole of the outer edge of the foot. Perhaps the boundary above the inner malleolus is a little lower this time than usual."

Ribs and lumbar vertebræ normal in number.

VIIth Post-thoracic.

Experiment.—*M. rhesus.* Male; young. 27.10.1890.

Dimensions taken, *vide post.*

At 9.40 the XIth and XIIth thoracic, the Ist, IIIth, IVth, Vth, and VIth post-thoracic roots of the right side severed.

At 4.40 the edge formed by the combined field of VIIth and VIIIth and IXth post-thoracic roots finally determined.

"The limit of the posterior field of reply is a line which starts from a point in the mid-dorsal line about 4 centims. below the level of the anterior superior iliac spine. From that point it passes outwards and downwards, so that it lies more than 1 centim. in front and above the prominence of the great trochanter. It then turns downwards and backwards, crossing the shaft of the femur at about the junction of its highest and second quarters to descend well behind the outer condyle and in the semiflexed position of the knee about ·5 centim. behind the head of the fibula, crossing over the outer head of the gastrocnemius, and striking the suro-peroneal crease about half-way down the leg. It then runs close along the fibula and over the external malleolus along the middle of the dorsum pedis, where it becomes less sharp and distinct. In the sole it is found on the lateral aspect of the 1st digit at the side of the proximal phalanx, and following the edge of the interdigital web of the first space, it crosses boldly along the top of the eminence of the muscles of the hallux, and back to the posterior part of the inner malleolus. It thus divides the plantar surface into a somewhat scanty medial third, and a liberal lateral two-thirds, leaving the unhairy sole over the side of the calcaneum at a point about the junction of the most posterior with the next quarter of the inner edge of the foot. Ascending the leg it lies in the lower half of the leg, close behind the subcutaneous surface of the tibia, but it is curved in harmony with the contour of the inner head of the gastrocnemius muscle. It meets the thigh along the edge of the fold caused by the prominent posterior edge of the sartorius. Keeping to the posterior border of the inner aspect of the thigh it ascends to the pubic notch, reaching it on its ventral face."

The relative shares of the VIIth, VIIIth, and IXth roots in this line will be discussed later on.

Ribs and lumbar vertebræ are normal in number.

VIIIth Post-thoracic.

Experiment.—*M. rhesus.* Female. 31.12.1890. Plate 46, fig. 14.

[illegible] posterior roots of the IIIrd, IV, Vth, VIth, VIIIth, and IXth post-thoracic roots of the

At 1.40 the cutaneous field of the VIIth post-thoracic root delimited completely.

"The isolated field of reply is marked out by a line which has been traced from the plantar surface of the web between the 1st and 2nd digits, and runs along the middle of the ridge over the plantar muscles of the hallux to the groove on the inner side of the heel, tends up behind the inner malleolus along the inner edge of the flexor aspect of the leg, and behind the inner condyle, following the inner border of the thigh almost to the top of the thigh. It then turns backwards and upwards forming a short horn, and, keeping well lateral to the ischial callosity, runs upwards, and then bends inwards as if to reach the mid-dorsal line. It falls short of that line by suddenly recurving once more when it has approached about as far as a vertical let fall upon the ischial callosity. The second turn upon itself forms a long horn, the outer edge of which lies about midway between the anterior and posterior edges of the outer aspect of the thigh. The line then descends the thigh, inclining more and more to the posterior aspect of it. It then skirts along the outer edge of the calf, and slopes somewhat forward so as to run over the dorsum and reach the root of the second digit, and the point whence it was traced."

Ribs and vertebræ normal in number.

VIIth Post-thoracic.

Experiment.—*M. rhesus.* Female. 22.9.1890.

At 10.45 the IVth, Vth, VIth, VIIIth, and IXth post-thoracic roots (posterior divisions) divided on the right side.

At 2.10 the delimitation of the cutaneous field of the VIIth post-thoracic root completed.

Delimitation of the area of the VIIth post-thoracic nerve-root.

"The isolated field of reply is a long strip reaching from the hip to the end of the 3rd digit. Its boundary is traced as a line which may be followed from a point on the front of the ankle close outside the tendon of the tibialis anticus muscle, along the 2nd intermetatarsal space to the web between the 2nd and 3rd digits, and then along the dorsum of the 2nd digit and to the plantar aspect of that digit, and outward along the web between the 2nd digit and the hallux, and over the prominence of the plantar muscles of the hallux and the medial edge of the sole to the groove between the internal malleolus and the heel. Thence it runs upward along the inner edge of the gastrocnemius and along the inner border of the thigh to the lower end of the genital fold. At that point it slopes backward and still inward, and attains to a little more than 1 centim. from the symphysis. It then takes a backward direction and climbs over the buttock somewhat more than 1 centim. lateral to the lateral edge of the ischial callosity. At a level about 2 centims. above the top of the callosity it turns inward toward the mid-dorsal line over the root of the tail, and circumscribes a blunt-ended, somewhat hook-shaped peak lying almost over the hip-joint. From the highest part of this peak, which is 8 centims. below the anterior superior spine of the ilium and somewhat nearer the mid-dorsal line than is that spine, the line sweeps down the limb on the external aspect of the thigh, and continually approaching nearer the posterior border of the thigh in its descent. From lying a little in the anterior half of that aspect above, it crosses into the posterior half of that aspect below, so that at the level of the knee it lies on the outer aspect of the outer hamstring. In its further descent it sweeps forward, following the contour of the outer head of the gastrocnemius, and then in front of the peroneal group to a point on the anterior aspect of the ankle about midway between the two malleoli."

Ribs and lumbar vertebræ normal in number.

VIIth Post-thoracic.

Experiment.—*M. rhesus.* Male. 27.10.1890.

Measured:—

Top of symphysis to xiphoid	17	centims.
Tip of 12th rib to anterior superior spine	5·5	„

The posterior divisions of the XIth, XIIth thoracic, the Ist, IIIrd, IVth, Vth, and VIth post-thoracic spinal nerves divided in the vertebral canal at 9.40.

At 6.10 the limits of the lower field of reply, mainly VIIth lumbar, determined.

"The lower field of response agrees closely with that found for the isolated VIIth lumbar root, on 22nd of last month. It is therefore mainly composed of VIIth, but VIIIth and IXth also come into it."

"Not so much of dorsum pedis as before."

Ribs and lumbar vertebræ normal in number.

*VIIIth Post-thoracic.**

Experiment.—*M. rhesus.* Female. 20.9.90.

At 9.10 A.M. the posterior roots of the Vth, VIth, VIIth, IXth, and Xth post-thoracic spinal nerves of the right side divided in the spinal canal.

At 11.15 the root of IVth lumbar of the right side divided also.

At 6.10 the determination of the field of the VIIIth post-thoracic completed.

"The isolated field of reply is contained by a line which can be traced as follows:—Starting from a point on the outside of the hip, about midway between the buttock and the inguinal fold, the line runs down the outer aspect of the thigh tending to pass to the posterior border of it. When on a level with the flexure of the ham it slopes inward more rapidly, and then descends on the calf to enclose a narrow tongue on the prominence of the calf and return over the inner hamstring, upwards, gradually encroaching on the inner border of the thigh. It ascends to the fold of the buttock and passes at an angle to its previous direction upward and backward on the medial side of the ischial callosity, and a short distance lateral to the root of the tail, to strike the point over the tip from which its course was traced."

"It was not until the IVth root had been severed that this area was isolated from the general upper field of reply, which latter field swept downward over the front of the thigh. After that last section the lower limit retired sufficiently to uncover the field of response that was then completely isolated, *i.e.*, that of VIIIth post-thoracic."

Ribs and lumbar vertebræ normal in number.

*VIIIth Post-thoracic.**

Experiment.—*M. rhesus.* Female; rather large. 24.9.1890.

At 12.45 the posterior divisions of the IVth, Vth, VIth, VIIth, IXth, and Xth post-thoracic spinal nerves divided on the right side in the vertebral canal.

At 6.30 the delimitation of the field of cutaneous distribution of the VIIIth post-thoracic root was finally complete.

"The isolated field of reply is a roughly quadrilateral patch. It is contained by a boundary which is traceable as follows.—Starting from a point on the extero-posterior aspect of the thigh on a level with the root of the tail, about 7 centims. below the level of the anterior superior spine of the ilium, and 4 centims. above the upper edge of the ischial callosity, and in a vertical falling ·6 centim. outside the lateral edge of the callosity, the line runs along the middle of the extero-posterior aspect of the thigh to a point somewhat behind the middle of the external surface of the knee, so as to be a little nearer to the free edge of the fold over the outer-hamstrings than to the external border of the patella. The line then turns backward and downward, encloses a tongue-shaped extension on the upper part of the belly of the gastrocnemius, and re-ascends to the fold of the inner hamstrings and follows that fold to reach the surface of the adductor group and then the inner aspect of the thigh, rising in a little triangular extension on the front of the genital fold, and then attaining the mid-ventral line in the angle of [illegible] pubis. It laps across the median line but slightly as judged from the other side. It is found finally springing from the side of the vulval orifice about half-way between the anterior and posterior ends of that orifice and running outwards in an almost straight line, touching the posterior angle of the callosity, and reaching the point whence it was traced. This edge of the field is about parallel with the long axis of the callosity."

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* [illegible] also Experiment given with figs. 3, 4, on pp. 688, 689

The ribs and vertebræ normal in number.

IXth Post-thoracic.

Experiment.—*M. rhesus.* Female; young. 10.10.1890.

Measurements :—

Anterior superior spine of ilium to tip of last rib . . .	5·5 centims.
Umbilicus to pubic crest	7·5 "

The last thoracic and first two lumbar, and the IVth, Vth, VIth, VIIth, and VIIIth post-thoracic roots of the right side divided intraspinally at 11 o'clock.

At 4.30 the anterior border of the IXth post-thoracic root finally determined.

"The anterior limit of the gluteal field of reply is bounded by a line that can be traced from the mid-dorsal line, about on a level with the upper edge of the thigh when the hip joint is flexed. The line slants outward and downward, making at first an angle of about 18° with the transverse plane of the trunk. When about in the same vertical with the lateral end of the ischial callosity, it turns steeply downwards as far as a point on a level with the root of the tail, and about as far above the ischial callosity as the length of the long diameter of the callosity. The line then slopes inwards and downwards, and running lateral to the outer angle of the callosity follows the lower edge of the callosity, and at about 1 centim. from the middle line of the perineum runs forward to the under and anterior aspect of the symphysis.

"The two areas, right and left, if joined would make a quadrilateral patch, with a superior angle and an inferior angle in the middle line of the body; the lateral angles at some distance either side the root of the tail."

Ribs and lumbar vertebræ normal in number.

IXth Post-thoracic.

Experiment.—*M. rhesus.* Male. 19.10.1890. Fig. 5, next page.

Measurements not taken.

The posterior roots of the IIIrd, IVth, Vth, VIIth, and VIIIth post-thoracic spinal nerves of the right side divided in the vertebral canal at 10.10 A.M. At 6.30 the anterior edge of the IXth post-thoracic segmental field delimited.

"The anterior edge of the hinder field of reply is traced from the side of the genital flap to the outer side of the ischial callosity, and thence upwards and outwards along the outer edge of the callosity to sweep round the buttock as if it were the arc of a circle whose centre lay at the root of the tail, and finally attain the mid-dorsum about 2 centims. below the point at which the lower edge of the upper field of reply (the IInd lumbar root) attains it." (Fig. 5.)

IXth Post-thoracic.

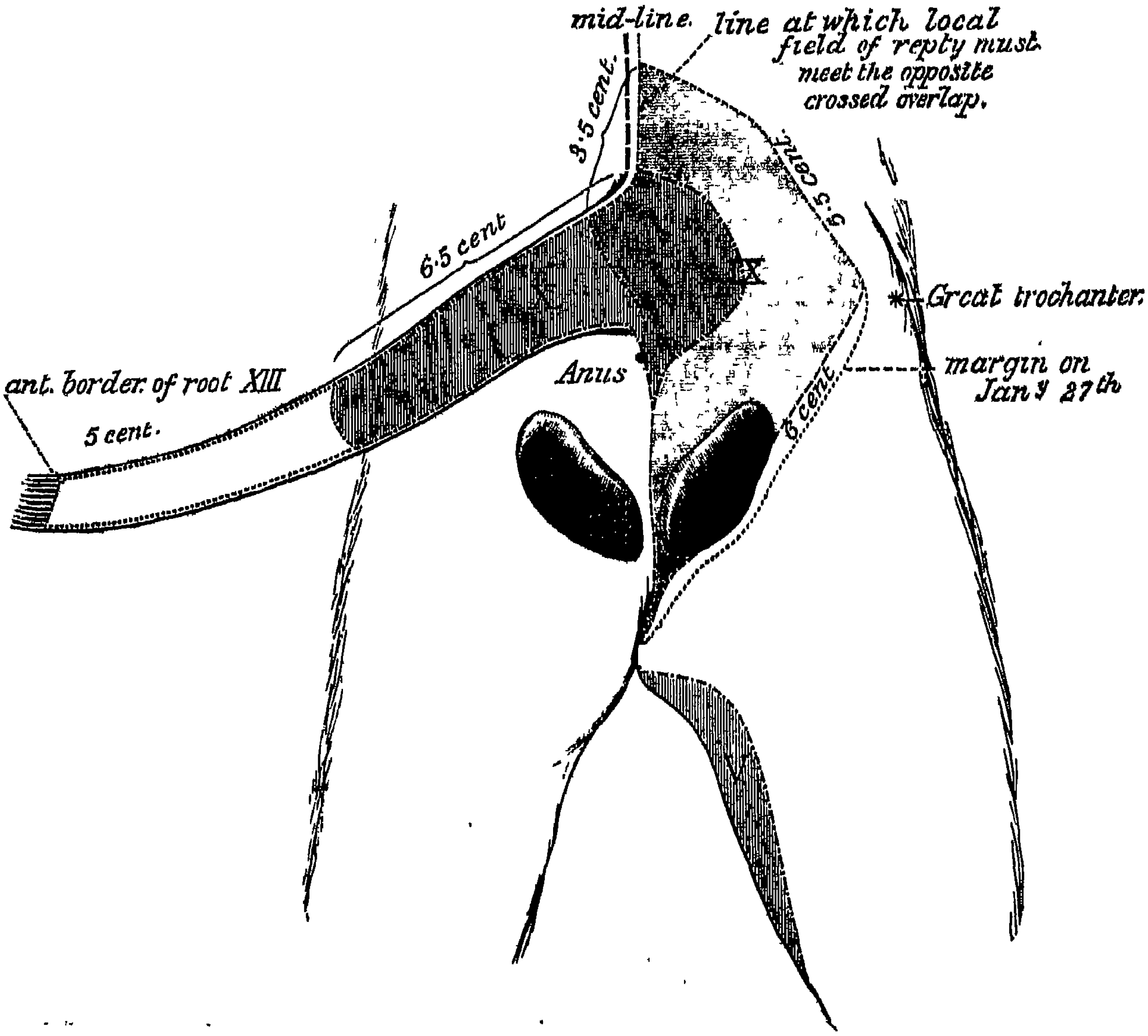
Experiment.—*M. rhesus.* Male. 27.1.1891. Figs. 5 and 6, pp. 722, 723.

The posterior divisions (roots) of the IIIrd, IVth, Vth, VIIth, and VIIIth post-thoracic spinal nerves divided in the vertebral canal at 12.25 P.M. The anterior border of the IXth post-thoracic field delimited at 6.30.

"The upper edge of the lower field of reply starts from the mid-dorsal line about 5 centims. below the level of the anterior superior spine of the ilium; the lower edge of the upper field of reply starts from the mid-dorsal line about on a level with the anterior superior spine, and the level at which the upper edge of the lower field lies at the mid-dorsum is about midway between the anterior superior spine and the ischial tuberosity. From that point the margin runs outwards, at first sloping downwards, then sloping more abruptly, and then turning inwards and downwards, so as to sweep about ·5 centim. outside the lower and lateral edge of the callosity and then runs forward under the inner edge of thigh up on to the front of the trunk along the lateral edge of the scrotum nearly as high as the root of the penis; at the root of the penis it meets the field of the upper roots."

At 7.30 the Ist lumbar root was severed on right side.

Fig. 5.



Sketch (made at the time).

"The lower field of reply on scrotum extends to same points as before, and it is now clear that replies from the side of the penis and from the glans penis which were taken to be part of field of the upper roots belong to the lower roots. It is not clear that the little area of reply which extends along the side of the penis and one-half the glans composes a field quite continuous with the scrotal field, because the replies are not obtained from absolutely the root of the organ; the penile field and the scrotal field are nearly continuous, but not quite, in this individual."

The penile and scrotal fields disappeared on section of the IXth post-thoracic root.

IXth Post-thoracic.

Experiment.—*M. rhesus.* Female; older. 12.11.1890. Plate 45, fig. 11.

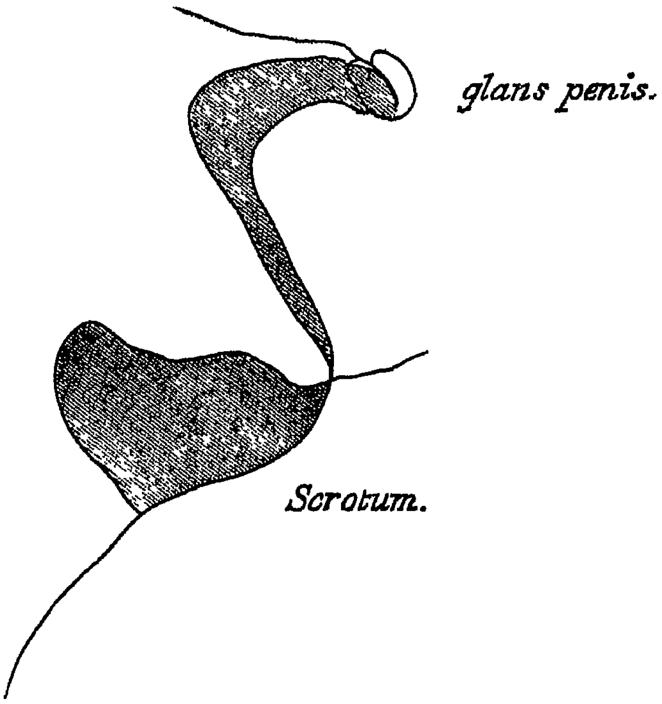
Dimensions: *vide* p. 702.

[illegible] VIth, VIIIth, Xth, and XIth post-thoracic roots of the right side severed

At 5 o'clock the lower of the two isolated fields (that of the IXth post-thoracic) delimited for the last time.

"The lower of the two isolated fields of reply is of roughly rhomboidal shape. Its anterior edge starts from the mid-dorsal line at a point on a level about with the mid-point between the top of the iliac crest and the summit of the great trochanter, a point which is in this specimen about 2·5 centims. above the top of the great trochanter. The boundary slopes outward and backward, inclining with a slight convexity forward, to a point less than 3 millims. on the medial side of the posterior edge of the great trochanter, and on a level ·6 centim. behind the upper border of the great trochanter. A line drawn across from this point on the right side to a similar on the left passes above the anus and just under the root of the tail. From the point so described it slopes backward and inward to reach the mid-ventral line about ·4 centim. in front of the anterior end of the vaginal aperture, reaching this point by passing along the lower border of the ischial callosity.

Fig. 6.



Sketch (at the time).

"The posterior edge of this isolated field of reply is an arc which starts from the mid-dorsal line 3·5 centims. behind the anterior edge of the field, reaches near to the mid-ventral line at the root of the tail and attains the mid-ventral line at the dorsal edge of the anus."

Ribs and lumbar vertebræ normal in number (fig. 7).

IXth Post-thoracic.

Experiment.—*M. rhesus.* Female. 30.7.1890. Fig. 7, next page.

At 9.5 A.M. two of the post-thoracic roots divided in the vertebral canal, one on right side, one on left, the left-hand one is one segment lower than the right-side one. *Post-mortem* dissection showed these roots to be the VIIIth of right side, the IXth of the left side.

On following morning, at 12.30, examination of the skin by touching and pinching, revealed same condition as on the previous afternoon.

"No complete absence of sensation can be detected. But there is a distinct blunting of sensibility over a small quadrilateral area to the left of the root of the tail, and over a larger triangular area with its base at the right ischial callosity, and a tapering apex pointed down the back of the thigh."

Number of ribs and of lumbar vertebræ normal.

IXth Post-thoracic.

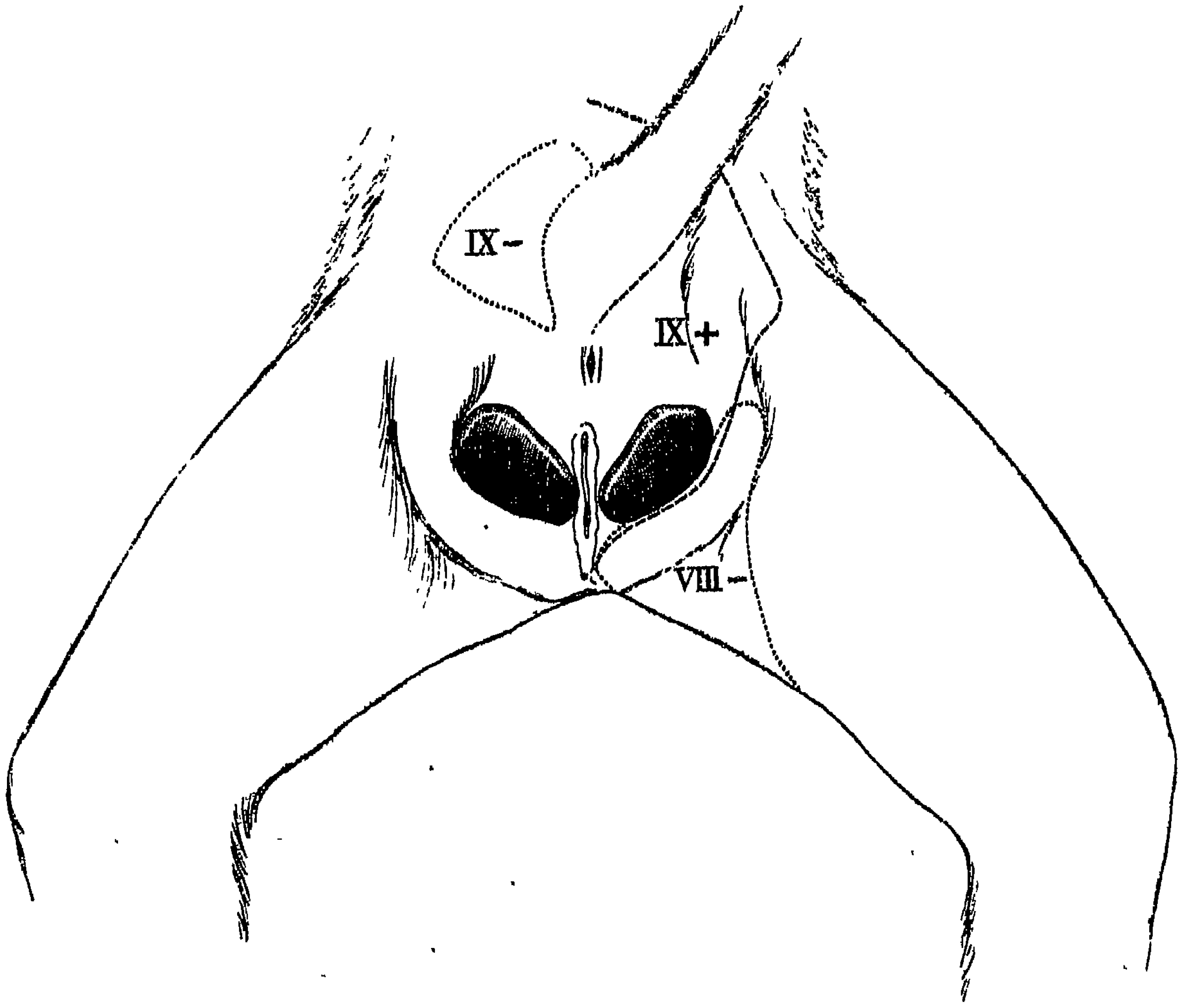
Experiment.—*M. rhesus.* Female. 4.4.1891.

At 8.50 the posterior roots of the XIIth thoracic, and Ist, IInd, IIIrd, IVth, Vth, VIth, VIIth, VIIIth, Xth, XIth post-thoracic spinal nerves divided.

At 1.50 the area of the Xth post-thoracic completely delimited.

"The field of reply is undoubtedly that of the Xth post-thoracic, for it agrees accurately with previous delimitations of that field. It passes from the dorsal crossed overlap above the root of the tail, and has a straight edge for some 7 centims. Then it turns backward at little greater than a right angle, and reaches the skin to the lateral side of the ischial callosity. It runs outside and below that callosity, and runs over the edge of the genital fold towards the front of the pubes, and then reaches the ventral crossed overlap."

Fig. 7.



The field of response (+) of root IX is sketched from the individual of 12.11.1890.

IX—. Patch where sensibility is obviously lowered after section of root IX.
VIII—. Similar patch after section of root VIII.
IX +. The field of response belonging to root IX.

"Behind, the edge of the field runs from the dorsal crossed overlap round the tail, close posterior [illegible] root of it, and reaches the ventral crossed overlap just above the anus. At the mid-ventral [illegible] the whole side of the labium vulvæ."

[illegible] in number.

Xth Post-thoracic.

Experiment. *M. rhesus.* Female; young. 19.5.1891.

At 10.15 the IVth, Vth, VIth, VIIth, VIIIth, IXth, XIth, and XIIth post-thoracic roots severed on the right side.

At 4.30 the area of cutaneous distribution of the Xth post-thoracic segment delimited finally.

"The limit of the isolated field of reply starts from the mid-dorsal line, close above the root of the tail, at a level a little above halfway between the posterior inferior spine of the ilium and the upper border of the callosity (*i.e.*, tuber ischii), sweeps downwards and outwards, with its concavity toward the root of the tail, to a point a little farther lateral than the middle of a line from the anus to the top of the great trochanter. Bending inward from that point, almost at a right angle, it follows fairly closely the line above mentioned toward the anus, but presently leaves it to meet the *labium vulvæ* about ·4 centim. from the posterior commissure."

"The posterior edge of the isolated field is a semicircle passing from the mid-dorsal line to the mid-ventral line on the tail, close behind the junction of the most anterior with the 2nd quarter of the length of the tail."

Xth Post-thoracic.

Experiment.—*M. rhesus.* Female; young. 31.10.1890.

Dimensions not taken.

The IInd, IIIrd, IVth, VIth, VIIth, VIIIth, and IXth post-thoracic roots of the right side severed at 8.50 A.M.

The XIth and XIIth roots severed at 5 o'clock.

The anterior border of the cutaneous field of the Xth post-thoracic finally defined at 4.30, about.

"The upper edge of the lower field of reply is limited by a line passing from the mid-dorsal line, just above the root of the tail, at a level about midway between the posterior inferior iliac spine and the upper border of the callosity; and from that point sweeps down and outward, then downward, then downward and inward, and attains the mid-ventral line at the posterior angle of the vaginal orifice. It is notable that although only one root was divided, there is about 3 centims. down the tail a semicircular zone of depressed reflex reply, so that the overlap of the skin fields seems less on tail than trunk and extremity."

At 6.30 the posterior border delimited.

"A semi-circular zone of greatly lowered response lies at the junction of the 1st and 2nd quarters of the tail. It is not strictly semicircular, but about one-third of a circle in extent, and about ·8 centim. wide. It is on the right side of the tail."

Ribs and lumbar vertebræ normal in number.

Xth Post-thoracic.

Experiment.—*M. rhesus.* Male; young; testes undescended. 29.10.90. Fig. 5, p. 722.

Measurements:—From xiphoid to the top of the symphysis pubis is 17 centims.

At 11.10 the VIth, VIIth, VIIIth, IXth, XIth, and XIIth post-thoracic roots of the right side severed.

At 4.50 the field of cutaneous distribution of the Xth post-thoracic root delimited for the last time.

The anterior edge of the isolated field of reply starts from the mid-dorsal line, just above the root of the tail; sweeping downwards and outwards it curves round the root of the tail, so as to turn inwards towards the anal orifice about 1·5 centim. above the callosity. When on a level with the anal orifice it lies about ·5 centim. above the level of the highest point of the callosity, and above ·8 centim. from the anal aperture; then it descends and runs forward, reaching the raphe about 1 centim. in front of the anus."

"The posterior edge of the isolated field of reply starts from the mid-dorsal line, upon the tail, 6 centims. from the root of the tail; it sweeps round from the dorsum to the venter, and there is a considerable crossed overlap, as judged from the distance which the anæsthetic skin field falls short of the mid-dorsal line and mid-ventral line, at least 4 millims."

Autopsy verified the normal number of thoracic and lumbar roots.

Xth Post-thoracic.

Experiment.—*M. rhesus.* Female; young. 19.11.1890.

Measurements as on p. 711.

At 12.15 the Ist, IInd, IIIrd, and the Vth, VIth, VIIth, VIIIth, and IXth post-thoracic roots of the right side severed.

At 5.20 the anterior border of the cutaneous field of the Xth post-thoracic root determined finally.

"The anterior edge of the posterior field of reply starts from the mid-dorsal line, 1 centim. behind the posterior border of the isolated field of reply (IVth lumbar) and runs outward for 38 centims., approaching as it does so to ·4 centim. of the posterior border of the isolated field of reply (IVth lumbar). It then turns abruptly backwards towards the callosity."

Ribs and lumbar vertebræ normal in number.

Xth Post-thoracic.

Experiment.—*M. rhesus.* Male. 3.11.1890.

Measurements:—

Anterior superior spine of ilium to the ligamentum patellæ	18 centims.
Symphysis pubis to umbilicus	8·5 ,,

Anterior border of the Xth post-thoracic root-field. The IIIrd, IVth, VIth, VIIth, VIIIth, and IXth post-thoracic, and later the IInd post-thoracic root severed in the spinal canal. The anterior border of the Xth post-thoracic determined finally at 5.20, about.

"The outer edge of the gluteal field of response can be traced from the mid-ventral line at the side of the penis, backward over the scrotum, and internal to the ischial callosity between it and the anus, and then encircles the root of the tail to meet a point on the mid-dorsum immediately above the root of the tail."

Xth Post-thoracic.

Experiment.—*M. rhesus.* Female. 25.10.1890.

The posterior divisions of the IVth, Vth, VIIth, VIIIth, and IXth post-thoracic spinal nerve of the right side divided in the vertebral canal at 11.15.

At 8.15 the field of cutaneous distribution of the Xth post-thoracic root was delimited for the last time.

"The anterior edge of the lower field of reply starts from the dorsal crossed overlap about 1 centim. behind the lower edge of the upper field of reply. It passes outwards almost horizontally, and nearly meets the upper field, and then curves backward and reaches the outer angle of the ischial callosity."

The upper field of reply was here the IIIrd lumbar, and for the Xth post-thoracic to approach so close to the IIIrd is quite unusual. The Xth post-thoracic in this individual extended more anteriorly [illegible] forward and toward great trochanter) and less far posteriorly on tail than usual. It included [illegible] Vth and IVth also. The number of ribs and of lumbar vertebræ was [illegible] lumbo-sacral plexus was found on dissection to be markedly post-fixed.

XIth Post-thoracic.

Experiment.—*M. rhesus.* Male; young. 24.11.1890. Plate 44, fig. 7.

Measurements:—

Pubes to infrasternal notch	16 centims.
Vertical distance from nipple to anterior superior spine of ilium .	14 „

The two lowest thoracic and the IInd, IIIrd, IVth, VIth, VIIth, VIIIth, IXth, and Xth post-thoracic roots divided intraspinally at 9.10 A.M.

At 5 the anterior border of the XIth post-thoracic root determined.

"The anterior edge of the tail field of reply is a line that runs round the side of the tail, from mid-dorsal line to mid-ventral line, at about the junction of the most proximal with the 2nd quarter of the tail. In front of it there is evidence of a good half-centimetre crossed overlap both ventrally and dorsally."

XIth Post-thoracic.

Experiment.—*M. rhesus.* Female. 12.11.1890. Plate 45, fig. 11.

Detailed above, gave practically the same result as regards anterior edge of the XIth post-thoracic as did the experiment above.

XIth Post-thoracic.

Experiment.—*M. rhesus.* 24.9.1890.

In which the IVth, Vth, VIth, VIIth, IXth and Xth post-thoracic roots were divided, gave practically the same result as the above two in November.

XIIIth Post-thoracic.

Experiment.—*M. rhesus.* Male. 29.10.90.

Measurements, *vide* p. 712.

At 11.10 the VIth, VIIth, VIIIth, IXth, XIth, and XIIth roots of the right side severed.

At 6 o'clock the anterior edge of the cutaneous field of the XIIIth post-thoracic ascertained finally.

"The anterior edge of the field of reply, which includes the tip of the tail, runs round the tail from mid-dorsal line to mid-ventral line 14·5 centims. from the root of the tail, 7 centims. behind the posterior edge of the isolated skin field." (Xth post-thoracic root.)

Vth Post-thoracic.

Experiment.—*Cat.* Female; young. 19.1.1891.

Delimitation of the field of the Vth lumbar root of the right side.

10.30. The Ist, IInd, IIIrd, IVth, VIth, VIIth, VIIIth, and IXth post-thoracic nerves (posterior roots only) divided on the right side.

At 1.30 the cutaneous field finally delimited.

"A triangular field with the base upward, above the knee, and occupying chiefly the outer side of the thigh, the inner aspect of the leg, the inner side of the foot more than half-way to the toes. A deep notch in the upper border (base) of the triangular field extends towards the inner side of the knee. The minimal reply obtained in the testing was always flexion of the toes."

Later, by excitation of the anterior roots it was found that the arrangement of the motor side of the plexus was *prefixed* in character. Thus excitation of the IXth post-thoracic root gave no movement in the limb muscles at all, but closure and detrusion of anus and movement of tail. And this prefixture on efferent side of the plexus was accompanied by prefixture of the afferent fibres because the knee jerk was well retained after section of the posterior root of the VIth lumbar nerve, whereas section of that afferent root usually abolishes it. By dissection, the plexus was also found to be decidedly prefixed. The ribs were thirteen and the lumbar vertebræ seven, *i.e.*, both normal in number.

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Thoracic . . 1st < 4th 5th	691	22.6.1891.	
Thoracic . . . 1st < 5th 6th	692	25.5.1891.	
Thoracic . . . 2nd < 4th 7th	692	5.8.1891.	Plate 42, fig. 1.
Cervical . . . 5th / 2nd Thoracic . . . 2nd \ 6th	693	18.6.1891.	
Cervical . . . 6th < 2nd 3rd	693	10.6.1891.	
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Thoracic . . . 3rd < 3rd 7th	694	26.8.1891.	Plate 42, fig. 2.
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Thoracic . . . 4th < 3rd 7th	695	22.10.1891.	Plate 43, figs. 3 and 5.
Cervical . . . 7th < 3rd 4th	696	2.4.1891.	
Thoracic . . . 7th < 4th 10th	697	17.12.1890.	
[illegible] 8th < 3rd [illegible]	697	7.6.1891.	

INDEX to Experiments of Series II.—(continued).

Segmental number of the skin-field examined.	Page.	Date of experiment.	Reference number of plate or figure.
Thoracic . . . 1st < 4th 5th	697	22.6.1891.	
Thoracic . . . 6th < 5th 6th	698	25.5.1891.	
Thoracic . . . 6th < 3rd 9th	698	6.4.1891.	
Cervical . . . 5th / 2nd Thoracic . . . 2nd \ 6th	699	18.6.1891.	
Thoracic . . . 2nd < 4th 7th	699	5.8.1891.	
Thoracic . . . 7th < 4th 10th	699	17.12.1890.	Plate 43, figure 4.
Thoracic . . . 11th < 7th 8th	700	27.11.1890.	
Thoracic . . . 4th < 3rd 7th	700	22.10.1891.	
Thoracic . . . 3rd < 3rd 7th	701	26.8.1891.	Plate 42, figure 2.
Thoracic . . . 3rd < 7th 8th	701	28.5.1891.	
Thoracic . . . . . (8th 11th	702	8.6.1891.	
Thoracic . . . 6th < 3rd 9th	702	6.4.1891.	
Thoracic . . . 12th < 9th 4th	702	17.11.1890.	
Post-thoracic . 1st / 10th Post-thoracic . 5th \ 11th	703	24.11.1890.	Plate 44, figure 7.

INDEX to Experiments of Series II.—(continued).

Segmental number of the skin-field examined.	Page.	Date of Experiment.	Reference number of plate or figure.
4th Thoracic . . . 7th 10th	703	17.12.1890.	
10th Thoracic 2nd	703	15.10.1890.	
8th Thoracic 11th	704	8.6.1891.	
11th Post-thoracic . 3rd 9th	704	10.10.1890.	
12th Post-thoracic . 3rd Post-thoracic . 9th 11th	704	12.11.1890.	
9th Thoracic . . . 12th 4th	705	17.11.1890.	Plate 44, figure 8.
12th Post-thoracic . 3rd 10th	705	19.11.1890.	Plate 44, figure 6.
11th Post-thoracic . 3rd 12th 9th	705	7.1.1891.	
11th Post-thoracic . 3rd 12th 9th	706	12.11.1891.	Plate 45, figure 11.
1st Post-thoracic . 5th 10th	706	31.10.1891.	
10th Post-thoracic . 1st Post-thoracic . 5th 11th	706	24.11.1890.	Plate 44, figure 7.
1st Post-thoracic . 6th 9th	707	20.2.1891.	
1st Post-thoracic . 5th 11th	707	22.12.1890.	

INDEX to Experiments of Series II.—(continued).

Segmental number of the skin-field examined.	Page.	Date of Experiment.	Reference number of plate or figure.
10th Post-thoracic . 2nd 7th	707	27.10.1890.	
2nd Post-thoracic . 6th 9th	708	13.2.1891.	
1st Post-thoracic . 5th 2nd 10th	708	3.11.1890.	
2nd Post-thoracic . 6th 9th	709	19.10.1890.	
3rd Post-thoracic . 10th 13th	709	19.5.1891.	
12th Post-thoracic . 3rd Post-thoracic . 9th 11th	709	12.11.1890.	Plate 45, figure 11.
3rd Post-thoracic . 6th 10th	710	25.10.1890.	
11th Post-thoracic . 3rd 9th	710	10.11.1890.	
9th Thoracic . . . 12th 4th	711	17.11.1890.	Plate 44, figure 8.
9th Thoracic . . . 12th Post-thoracic . 4th 10th	711	19.11.1890.	Plate 44, figure 6.
3rd Post-thoracic . 8th 4th 11th	712	26.9.1890.	
5th Post-thoracic . 10th 13th	712	29.10.1890.	
10th Post-thoracic . 1st Post-thoracic . 5th 11th	713	24.11.1890.	Plate 44, figure 7.

INDEX to Experiments of Series II.—(continued).

Segmental number of the skin-field examined.	Page.	Date of experiment.	Reference number of plate or figure.
Post-thoracic . $5\text{th}\left\langle\begin{matrix}1\text{st}\\10\text{th}\end{matrix}\right.$	713	31.10.1890.	Plate 46, figure 12.
Post-thoracic . $5\text{th}\left\langle\begin{matrix}1\text{st}\\11\text{th}\end{matrix}\right.$	714	22.12.1890.	
Post-thoracic . $1\text{st}\diagup 9\text{th}$ Post-thoracic . $5\text{th}\diagdown 11\text{th}$	715	29.12.1890.	
Post-thoracic . $5\text{th}\left\langle\begin{matrix}1\text{st}\\2\text{nd}\\10\text{th}\end{matrix}\right.$	715	3.11.1890.	
Post-thoracic . $6\text{th}\left\langle\begin{matrix}12\text{th}\\10\text{th}\end{matrix}\right.$	715	27.1.1891.	Plate 45, figures 9 and 10.
Post-thoracic . $6\text{th}\left\langle\begin{matrix}2\text{nd}\\9\text{th}\end{matrix}\right.$	716	19.10.1890.	
Post-thoracic . $6\text{th}\left\langle\begin{matrix}3\text{rd}\\10\text{th}\end{matrix}\right.$	716	25.10.1890.	
Post-thoracic . $6\text{th}\left\langle\begin{matrix}2\text{nd}\\9\text{th}\end{matrix}\right.$	717	13.2.1891.	
Post-thoracic . $6\text{th}\left\langle\begin{matrix}1\text{st}\\9\text{th}\end{matrix}\right.$	717	20.2.1891.	Plate 46, figure 13.
Post-thoracic . $6\text{th}\left\langle\begin{matrix}2\text{nd}\\10\text{th}\end{matrix}\right.$	718	16.3.1891.	
Post-thoracic . $2\text{nd}\left\langle\begin{matrix}10\text{th}\\7\text{th}\end{matrix}\right.$	718	27.10.1890.	
Post-thoracic . $7\text{th}\left\langle\begin{matrix}2\text{nd}\\10\text{th}\end{matrix}\right.$	718	31.12.1890.	Plate 46, figure 14.
Post-thoracic . $7\text{th}\left\langle\begin{matrix}3\text{rd}\\10\text{th}\end{matrix}\right.$	719	22.9.1890.	
Post-thoracic . $2\text{nd}\left\langle\begin{matrix}10\text{th}\\7\text{th}\end{matrix}\right.$	719	27.10.1890.	

INDEX to Experiments of Series II.—(continued).

Segmental number of the skin-field examined.	Page.	Date of experiment.	Reference number of plate or figure.
Post-thoracic . **8th** < 3rd 4th 11th	720	20.9.1890.	
Post-thoracic . **8th** < 3rd 11th	720	24.9.1890.	
Post-thoracic . 3rd < 11th **9th**	721	10.10.1890.	
Post-thoracic . 6th < 2nd **9th**	721	19.10.1890.	Figure 5, p. 722.
Post-thoracic . 6th < 2nd **9th**	721	27.1.1891.	Figures 5 and 6, pp. 722, 723, and Plate 47.
Post-thoracic . 3rd < 12th **9th**	722	12.11.1890.	Plate 45, figure 11, and figure 7, p. 724.
Post-thoracic . . . (8th **9th**	723	30.7.1890.	Figure 7, p. 724.
Post-thoracic . **9th** < 11th 13th	724	4.4.1891.	
Post-thoracic . **10th** < 3rd 13th	725	19.5.1891.	
Post-thoracic . 5th / 1st Post-thoracic . **10th** \ 13th	725	31.10.1890.	Plate 46, figure 12.
Post-thoracic . **10th** < 5th 13th	725	29.10.1890.	Figure 5, p. 722, and Plate 46.
Post-thoracic . 4th < 12th **10th**	726	19.11.1890.	
Post-thoracic . 5th < 1st 2nd **10th**	726	3.11.1890.	
Post-thoracic . 6th < 3rd **10th**	726	25.10.1890.	

INDEX to Experiments of Series II.—(continued).

Segmental number of the skin-field examined.	Page.	Date of experiment.	Reference number of plate or figure.
10th Post-thoracic . 1st Post-thoracic . 5th 11th	727	24.11.1890.	Plate 44, figure 7.
10th Post-thoracic . 1st Post-thoracic . 5th 11th	727	25.11.1890.	Plate 45, figure 11.
1st Post-thoracic . 8th 11th	727	24.9.1890.	
5th Post-thoracic . 10th 13th	727	29.10.1890.	
3rd Post-thoracic . 8th 11th	688	4.5.1891.	Figures 3 and 4, pp. 688, 689.
Cat—			
12th Post-thoracic . 5th 10th	727	19.1.1891.	

CONCLUSIONS.

When the facts of the above arrangement are compared with those found to exist in the Frog (*v. supra*, p. 652, &c.), it will be seen that considerable differences between the two schemes of distribution become apparent. It seems well to return to the conclusions arrived at for *Rana*, and examine the extent of their applicability to *Macacus*.

1. Although in a plexus each spinal nerve-root affords separate contributions to many several nerve-trunks in the plexus, the cutaneous distribution of the root is composed, not of patches which are disjoined, but of patches which are so joined that the distribution of the entire root forms one continuous field.

Looking over the areas determined for *Macacus* in the foregoing experiments, it is seen that, just as in the leg of the Frog, so with the nerve-roots of the trunk and lower limb of *M. rhesus*, each root possesses a single undivided field of cutaneous distribution, not a field composed of separated patches. This is a point to which attention was always paid in the experiments, because it was remembered that TÜRCK found evidence of such "divided" fields in the case of certain nerve-roots, viz., the IInd and IIIrd thoracic roots of the Dog; also because such an arrangement might exist with the more complexly branched plexus of *Macacus*, although absent from the simpler type of the Frog. In *Macacus* no evidence of this division of the skin-field of the root was found. There was once noticed, it is true, in an experiment upon the IInd thoracic root, a small area, about an inch long,* which *appeared* to be not perfectly continuous with the otherwise perfectly continuous field of reply referable to that root; but this outlying islet did not appear in other delimitations of the IInd thoracic field, and it was well within the limits of error which must be acknowledged for the experiments. My experimental fields probably understate, perhaps in certain directions considerably, the real area of skin-field of the root. The above apparent exception to the general statement is, therefore, mentioned, but is not believed to really modify the statement. Another instance of an outlying islet of æsthesia, apparently detached from the general field at the rest of the root, occurred in an experiment on the IXth post-thoracic. One-half of the scrotum is included in the field of the IXth post-thoracic, and also the corresponding half of the penis, but I could not demonstrate the conjunction of the scrotal and penile fields at the root of the penis.† I think this probably due to my experimental field being a minimal representation of the true root-field, and that probably the skin at the root of the penis is included in the root-field, and through it the penile and scrotal fields are conjoined.

Similarity of the root compositions of neighbouring nerve-twigs that are near their destination is a necessity of the above arrangement. Thus, the dorsal collateral digital nerve on the tibial side of a digit will resemble in composition the plantar collateral digital on the tibial side of the same digit, and this is exemplified in the table of analysis of peripheral nerves given above. This is comparable to the similarity of root composition exhibited by the several motor twigs entering a skeletal muscle in the limb. Thus, the tibialis anticus receives fibres from the anterior roots of at least two spinal nerves entering the plexus, and receives those fibres by several separate nerve-branches entering the muscle; in each of the nerve-branches will be found a proportion of fibres from each of the roots supplying the muscle, and in fairly similar proportions in all. But there are exceptions, thus the upper and lower nerves to the sartorius, the upper nerves containing the fibres from the IIIrd and IVth lumbar roots, the lower from the IVth and Vth lumbar roots. So also adductor magnus.

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* *Cf.* Photograph 1, Plate 42.

† *Vide* sketch, (fig. 6, p 723).

On the dorsum of the foot a somewhat curious anatomical arrangement of the peripheral nerves to the skin of the toes is the interposition between the digitales communes from the musculo-cutaneous trunk of a similar trunk for the cleft between hallux and 2nd digit supplied from the anterior tibial nerve. I looked with some interest to see whether the root composition of the branch from the anterior tibial would fall into series with the arrangement of the root composition of the digitals from the musculo-cutaneous. In the latter, as traced from the tibial toward the fibular edge of the foot, *i.e.*, from the preaxial toward the postaxial border, the proportion of fibres from the Vth lumbar root rapidly diminishes to disappearance, a proportion of fibres from the VIIth lumbar root appears and gradually increases. In *Rhesus* (and also in Cat) experiments disclose (pp. 668 and 679) that the branch from the anterior tibial falls into perfect series with the rest as far as its root composition is concerned, and can be analysed by the experiments above. The case is comparable with that of the external saphenous nerve in *Macacus* and the plantar muscles.* Despite the existence of some latitude of individual variation (*vide infra*), the connection between the position of the central end of a sensory nerve fibre and that of the peripheral end is, in one and the same individual, definite and fixed enough. In other words, the mutual relationship between the position of points composing a region of the body is specific, the absolute position of the whole region is largely individual.

2. The field of skin belonging to each sensory spinal nerve-root overlaps the skin fields of the neighbouring spinal nerve-roots to a remarkable extent. The disposition is such that the field laps to a certain extent over the field of the root or roots immediately in front of it, and to a certain extent over the field of the sensory roots immediately behind it. These two overlaps may be termed respectively the anterior overlap and the posterior overlap of the sensory root field. (See diagrams, Plate 52.)

The above conclusion is applicable without modification to the arrangement existing in *Macacus*. The overlap is very great, so great indeed that each point of skin is supplied by two spinal nerve-roots, and some, it would appear, by three. And this [illegible] for the nerves of the trunk as well as for those of the limb. Thus the nipple is a point of skin which lies in the field of the IVth thoracic root, often a little nearer the posterior than the anterior border of that field. Now the nipple is included also in the experimental field of the Vth thoracic root, the anterior border of which passes above it; and the nipple was found on two of three occasions on which the posterior border of the field of the IIIrd thoracic root was examined to lie demonstrably in the experimental field of that root, although on one occasion the border passed just above the nipple itself, including only the areola above the nipple. In the foot the mid-point of the border of the web between hallux and 2nd digit is included in the experimentally demonstrable field of the VIth lumbar root; it is also generally included in the experimentally demonstrable fields of the Vth lumbar and VIIth lumbar roots, but it lies at the very confines of those fields. The skin of the upper part of the ham is included in the fields of the VIIth and VIIIth post-thoracic roots.

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* Sherrington, 'Journ. of Phys.,' 13, p. 739.

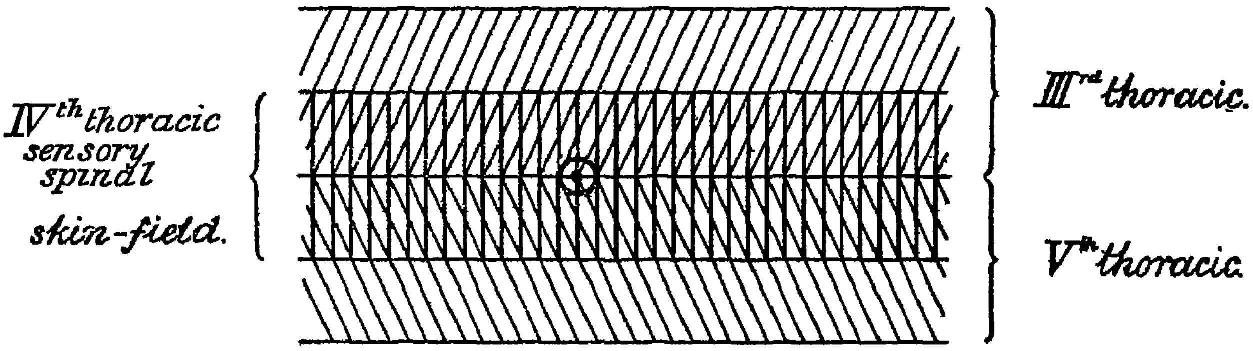

Diagram of the position of the nipple in the sensory skin-fields of the IVth, IIIrd and Vth thoracic spinal roots.

Acknowledging that the size of the experimental skin-fields is somewhat smaller than the size of the skin-fields in reality, I conclude that the anterior and posterior overlaps are extensive enough in the Monkey to provide that the skin, taken along any line parallel with the plane of segmentation of the body in the region in which the line is taken, is supplied by two adjacent posterior roots. It further seems certain that in certain places the skin is supplied by three adjacent posterior roots, more by the middle of the three roots, less by the foremost, and by the hindmost of the three roots individually taken. Possibly skin in which the interlap is thus triple instead of double exists along the centre of the cutaneous segments of the body. In the sole (Cat) the anterior border of the skin-field of the lowest of three* roots overlaps the posterior border of the skin-field of the highest root of the three. The amount of supply given to its skin-field by a given root appears to vary in different parts of the field, and it is usual for the border of the field to be less richly supplied than the rest of the field. Thus the nipple lies about midway in the field of the 4th cutaneous segment of the thorax, and it is in each normal individual probably supplied by the Vth thoracic and the IIIrd thoracic afferent roots, as well as by the IVth. It would therefore lie in one of the narrow zones of triple interlap above mentioned. I have met with an instance in which it was included in the anterior edge of the 6th thoracic skin-field.[*] In the trunk the degree of overlap of the skin-fields often seems to be less near the mid-dorsum and mid-ventral lines than on the lateral aspect at some distance from those lines. It must be remembered that the nipple lies in this lateral region, and so also, as I shall point out later, does the foot with its digits, again a region of remarkable overlapping.

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* These are VIth, VIIth, and VIIIth post-thoracic. See also Tables, pp. 668, 679, 685.

Beside the anterior and posterior overlaps, the cutaneous field of each posterior root oversteps the median line of the body both ventrally and dorsally. This crosslap of right and left-hand nerves is not so extensive as the overlap fore and aft. It is comparable with the lapping across the dorsal median line of the distribution of the pilomotor nerves in the Monkey and Cat as described by LANGLEY and myself.[†] It seems to vary in *Macacus* in different regions. It seems more marked along the mid-ventral line than along the mid-dorsal line, and I have seen it remarkably extensive on the penis, and close below the xiphoid. I do not think I have ever seen it amount to more than a full centimetre in *Macacus*, but all the specimens have been small and the crosslap might be larger in larger individuals. The amount of supply by the root to the cross-lapping border of the field appears relatively small compared to elsewhere in the field, in fact it resembles in this way the extreme border of the forelapping and afterlapping portions of the skin-field.

Where seen at its simplest, viz., in the thoracic region, the shape[‡] of the cutaneous field of the posterior root is that of a horizontal band with fairly parallel edges wrapping half round the body between the mid-dorsal and mid-ventral lines. In the lower half of the thorax each zone thus formed slopes somewhat, so that the ventral end of it appears to lie further caudal than the dorsal end of it. Each zone is narrowest at its dorsal end, and widest somewhere not far from its ventral end. The width of the individual zones gives us some idea as to how the external configuration of the body has been brought about. Where the body approaches a regular figure, a cylinder, a double cone, &c., the root-field is zonal, possessing long anterior and posterior sides fairly parallel each with the other, and short dorsal and ventral sides set approximately at right angles to the anterior and posterior. If the whole animal were a cylindrical, simple figure, this configuration of the root-field would presumably hold good for all its segments, as it presumably approximately does in such a form as *Amphioxus*. But where the animal form is less regular the simple zonal shape set fairly at right angles to the body axis is departed from in many ways. The antero-posterior width of the skin strip may be increased at one part or another by an extension forwards of the anterior border, or an extension backward of the posterior border. The ventral border may be thrown backwards and the skin strip thus come to be obliquely set. The anterior and posterior borders may become curved, and one of them be more curved than the other, or both of them be fairly similarly curved, so that their parallelism is still roughly maintained.

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[*] The difficulty is to estimate confidently the overlapping and the individual variation.

[†] 'Journal of Physiology,' 12, p. 278.

[‡] [illegible] hereafter, p. 749, see especially the areas as painted out on casts taken [illegible] inclusive. Also the diagrams on Plate 52.

If these departures from the simple zonal type of root-field afford a hint as to the modifications which body-segments have individually undergone in the development of the present configuration of the animal, it would seem that in the abdominal region of *Macacus rhesus* each root-field has become expanded at its ventral end. Also one can notice in *Macacus rhesus* that in the region of the abdomen and the loin the zonal root-fields are individually wider than in the thoracic region. The mid-ventral line, from the top of the sternum to the pubes, is seen to correspond segmentally with the mid-dorsal line along the region of the thoracic vertebræ. The length of that portion of the mid-ventral line was 31 centims. in an individual in which the corresponding portion of the mid-dorsal line measured only 21 centims. It is seen that that is explicable by the ventral ends of the root fields being wider than the dorsal ends of them, and that the difference is greatest for the lowest two thoracic and the highest lumbar segments.

In the animal body the greatest departure from a simple and regular figure is caused in the vertebrate forms by the excrescence of the limbs. How does the segmentation of the body behave in the region of the limbs? In the Frog it has been shown above that the simple zonal character of the root-fields, although disturbed in the hind limb, is not actually departed from and is still easy to perceive. "The cutaneous field for each posterior root meets the middle line of the body both ventrally and dorsally." Each root-field sweeps down the limb and up again upon it, so that the free apex of the limb is by this test about equidistant from the mid-ventral and mid-dorsal lines; the digits are, in fact, so many points on the lateral line of the body, as they were shown to be at the earliest origin in the embryo. The most segmentally anterior portion of the skin of the hind-limb of the Frog is found to occupy the extensor aspect (front) of the thigh. Next come the extensor and peroneal aspects of the leg, then the dorsum pedis, the sole, the calf, and, finally, the most segmentally posterior is the flexor aspect (back) of the thigh. It is the comparatively small number of nerve-roots distributed to the hind limb of *Rana* that in its case makes the arrangement of such an obvious kind. The skin of the limb in *Rana* is supplied practically by four roots only.

Turning to *Macacus rhesus*, one finds that if the surface of the limb be considered to be bounded proximally by POUPART'S ligament, and by a line passing from the anterior superior spine backwards over the ischial tuberosity to the genital fold, the skin of the limb has eight roots contributing to its supply.

A salient difference between the distribution of the skin-fields of these, and that of the root-fields in the hind limb of *Rana*, is that in the case of the former certain root fields do not conform to the conclusion above drawn from *Rana;* that is, they do not meet the middle line of the body either ventrally or dorsally. The skin-field of the posterior root of the IVth lumbar nerve sweeps from the median line of the back, not to the median line of the belly, but to the inner edge of the thigh and leg. The field of the Vth lumbar is everywhere widely distant from the median line of the back and the median line of the belly. The field of the VIth lumbar is entirely confined to the distal portion of the limb. The field of the VIIth lumbar, also, is wholly separate from the median line of the back and belly. The field of the first sacral I have failed to find extending to the median line of the back, although in the female it does seem to reach the ventral median line upon the pubes. In other words, tracing downward the body segments of *Macacus*, as indicated by the cutaneous distribution of the sensory spinal roots, one finds, on arriving at the IVth lumbar segment, that the succeeding segments, as regards the skin, become entirely limb segments, and slip outwards down the limb, and then return upward upon it again, regaining the median line of the body completely only when the IInd sacral nerve is reached. Further than this, they leave the mid-dorsal line of the body nearly a segment lower than they leave the mid-ventral line. In each of the median lines of the body, the segments leave and return to the line at the same definite point. The position of this point in the mid-dorsal line of the body is decidedly below the level of midway between the anterior superior spine of the ilium and the bottom of the tuber ischii; in the mid-ventral line of the body the point is on the front of the pubes, and in the female appears to be lower down on the pubes than in the male.

To ascertain in what way the shape of the simple zonal root-field, which one has considered typical, is modified in the configuration of the limb, it is essential to discover the positions of the four borders of the field—the anterior, posterior, ventral, and dorsal. The distortion may have unequally affected these four borders. In order to do this one begins best, perhaps, by observing the position and character of the borders of these root-fields, which only partially contribute to the surface of the limb, and in which the dorsal and ventral borders obviously follow the mid-dorsal and mid-ventral lines of the body. The highest root-field to contribute to the limb is that of the Ist lumbar. This is distorted from the simple zonal form only in its ventral half, and its distortion is mainly caused by the extension backwards of its posterior border, so that it becomes much wider at its ventral end. Its posterior border thrusts also a curious shallow flap across the fold of the groin into the thigh over about the middle of POUPART'S ligament. The IInd lumbar root-field resembles in shape an exaggerated Ist lumbar field. The exaggeration of the flap down the extensor surface of the thigh is caused partly by the ventral end of the posterior border returning toward the pubes, and the flap may extend a full third of the way to the knee. In the IIIrd lumbar root-field the thigh flap assumes still greater proportions, and involves, at least, two-thirds of the whole posterior border. Its flap covers the [illegible] part of the whole anterior aspect of the thigh, and resembles somewhat the [illegible] cut in amputation above the knee. Just as in the case [illegible] so in the IIIrd lumbar the posterior border on median side of the flap retires again toward the mid-ventral line on the pubes. So far, then, the root-fields contribute to the surface of the limb by an extension from their posterior border in its lateral portion, lying somewhat more perhaps to the ventral than to the dorsal side of the mid-lateral line of the body.

The disposition of the contribution of the IVth lumbar skin-field to the limb is less simple to discover. The field sweeps from the median line of the back over the ilium, down the extensor face of the thigh, over the knee and inner face of highest part of the leg, to the inner border of the thigh, *i.e.*, the skin covering the gracilis, and to the inner line of attachment of the calf muscles. Its shape implies that the whole of the ventral portion of its posterior border has contributed to the limb in a flap still greater than that protruded from the posterior border of the preceding field. It is true that the border does, in the leg, curve slightly upwards again as if making for the pubes, but it falls far short of reaching it; it reaches only to the inner border of the thigh. Which of its periphery is therefore its ventral border? Before deciding, it must be seen if it is possible to trace the anterior border. That is easy. The anterior border sweeps obliquely downward and forward from the mid-dorsum, over the ilium, to follow the inguinal fold and reach the pubes. Opposite the outer part of POUPART'S ligament, it turns down the thigh for a short distance, just as did the anterior border of the Ist lumbar field at a slightly higher level. There is, therefore, in this position a notch downward into the posterior border of the IVth lumbar field, just as there was a shallow tongue downward from the anterior border of the Ist lumbar field. This notch may be taken to mean that the distortion of the root-field by the excrescence of the limb involves at the level of the IVth lumbar segment, not merely the posterior part of the field, but the entire antero-posterior depth of the root-field. Which is the ventral border? It is clear that the ventral border extends from the pubes below the knee along the skin covering the line of apposition of the adductor and flexor muscular groups of the thigh.

If one now, before examining the nature of the distortion of those four skin-fields in the limb that are completely detached from the trunk, examine the root-field immediately succeeding the detached fields, *i.e.*, IXth post-thoracic, it is seen that, encroaching little on the limb, the field in question is still attached to the mid-dorsal and mid-ventral lines of the trunk.

As is seen in fig. 17, Plate 48, figs. 23, 24, Plate 51, clearly the dorsal edge of the field follows the mid-dorsal line from a short distance above the root of the tail, and upon the tail, for a short way. It is also clear that the field has a ventral border at the mid-ventral line of the body from the upper edge of the anus to a few millimetres in front of the mesial end of the ischial callosity. Further, the posterior border of this field is easily distinguished as that edge of it which runs from the posterior end of the dorsal border to the posterior end of the ventral border, that is to say, partly round the half circumference of the tail, and down to the upper border of the anus. The posterior, dorsal, and ventral borders having thus been determined, the rest must be anterior border. But there is a curious character belonging to a part of the so-discovered anterior border. The border may be divided into two portions—a shorter or more dorsal portion, which passes from the anterior end of the indubitable dorsal border at the mid-dorsal line of the body on the sacrum, and extends as far as the root of the tail; and a longer remaining part, which runs from that point to the mid-ventral line of the body, and makes an angle little greater than a right angle with the dorsal part. Of these two pieces of the edge, the dorsal portion above defined does not behave as does the rest of the edge. The rest of the edge overlaps largely the skin-field of the root immediately preceding it, the VIIIth post-thoracic, and perhaps slightly the edge of the field of the VIIth post-thoracic. It behaves exactly as do the anterior borders of the root-fields examined elsewhere. The dorsal piece of the edge, on the contrary, does not lap over the field of the root immediately preceding it. It hardly overlaps any other root-field at all.

It may be truly described as coming into apposition with the root-field next it, its interlap with the root-field next it is no more extensive, or hardly so extensive as the crosslap of the fields of the right and left sides of the body at the mid-dorsum. The dorsal piece of the edge behaves as if it were a piece of the dorsal border of a field. And with what root-field does it come into contact? It comes into contact with the lowest field of those passing into the limb, but still attached to the mid-dorsum of the trunk, namely, with the skin-field of lumbar IV, a root situated five segments above it in the segmental series of the body. The intervening segments have, as it were, slipped down the limb, and left in contact the segments on either side of the gap, but those segments do not overlap in the ordinary degree of forelap and afterlap. It is natural to conclude, therefore, that the dorsal piece of what at first seems the anterior border of the IXth post-thoracic root-field does not really pertain to the anterior border, but, as regards the IXth field, is part of the mid-dorsal line. In the same way, therefore, a similar piece of what at first sight seems part of the posterior border of the skin-field of lumbar IV, is, as regards the IVth lumbar skin-field, part of the mid-dorsal line of the body.

A method by which the dorsal and ventral borders may be distinguished from the anterior and posterior borders of the segmental field consists in noting the degree to which the initial contraction of the field, followed by subsequent extension of the field, affects the various parts of its periphery respectively. The smartness of response in the field seems, as a broad rule, to which exceptions exist, to approach closer to the extreme dorsal and ventral borders, than to the extreme anterior and posterior borders. In like manner the degree in which extension of the field affects the anterior and posterior borders is much greater than that to which it affects the dorsal and ventral borders. (*Vide supra,* p. 687, and experiments on pp. 688, 689, [illegible] figs. 3 and 4.)

[illegible] a better position for determining the nature of the distortion [illegible] completely detached zonal fields in the excrescence of the limb. [illegible] skin-field resembles in figure an acute angled and rudely isosceles triangle, with the apex at the hallux, and the base on the front of the thigh exhibiting a deep notch in it. This notch is an exaggerated repetition of the similar notch seen in the anterior border of the IVth lumbar field. In order to determine the extent of this posterior border it is necessary to use the facts already found. One has found that in the case of the IVth lumbar field a piece of the dorsal edge turns outward over the ilio-sacrum to the thigh, that is to say, the mid-dorsal line of the body turns abruptly outward and begins to descend the outer aspect of the thigh. One has also found that the ventral border of the immediately preceding root-field, the IVth lumbar, instead of lying at the median line of the venter, lies at the median edge of the thigh, over the septum between the adductor and flexor muscle groups of the thigh. This, which may be termed the medial border of the thigh, is, therefore, as regards the segmentation of the skin, the continuation of the mid-ventral line of the body. In other words, just as at a certain point on the back the mid-dorsal line turns outward along the thigh, so at a certain point on the belly the mid-ventral line turns outward along the thigh. The crural extension of the mid-dorsal line descends along the medial border of the thigh. The true anterior border of the Vth lumbar field is now easy to determine. It leaves the mid-dorsal line of the limb at a point little more than half up the thigh, thence over the extensor muscle group, showing a deep inflexion kneeward as it does so, and finally meets the mid-ventral line of the limb on the adductor group in the most proximal quarter of the thigh. The posterior border of the Vth lumbar field sweeps from the mid-dorsal line of the limb on a level with the knee downward, over the outer aspect of the leg, and on the dorsum pedis passes lateral to the hallux (which is therefore included in the field of the Vth lumbar), and returning along the medial half of the sole of the foot ascends the groove internal to the tendo Achillis, attaining the mid-ventral line of the limb on the skin-fold over the inner hamstring tendons.

The Vth lumbar-field also helps one to extend the mid-dorsal and mid-ventral lines of the limb as low as the knee joint. The mid-dorsal line is found to descend to behind the head of the fibula; the mid-ventral line to follow the skin-fold over the inner hamstring tendons. The nature of the distortion which the Vth lumbar field has undergone is now seen to be as follows: it is a large field, but the distance between the dorsal and ventral borders of it is not so great as in the skin-fields of the thoracic roots (14 centims. as against 22 centims.). The dorsal and ventral borders are not much increased considering the large size of the field, just as in the case of the root-fields on the trunk the ventral border is longer than the dorsal. The distortion from a simple zonal shape is chiefly due to the protrusion of a great peak-shaped flap from the posterior border, which at its tip like the finger of a glove encloses the first digit. That the whole antero-posterior width of the root-field is implicated in this thrust downward is clearly indicated by the existence of the curved in-thrust of the anterior border downward corresponding to the opposite out-thrust of the peak-shaped flap.

The skin-field of lumbar VI possesses a distribution more apical than any other in the limb. The interpretation of its relation in shape to a simple zonal root-field is as follows: the anterior border passes from the mid-dorsal line of the limb at the outer side of the knee, to the mid-ventral line of the limb at the inner side of the knee. Instead of, like the anterior border of the Vth lumbar, being partially occupied by a notch, it is entirely involved in forming the sides of a huge inflexion which stretches from the level of the knee nearly to the ankle and has its retiring angle on the front of the inner face of the leg not far above the ankle joint. The posterior border of the field appears to be short, and extends from the mid-dorsal line of the limb about half-way up the thigh, across the flexor muscle-group to the mid-ventral line of the limb in the lower third of the thigh. It is not easy to determine where the posterior border joins the ventral border, partly because the line of direction of the two borders is so similar. It is also partly for the same reason not easy to determine the point at which the anterior border joins the ventral border. In fact, the exact limits of the ventral border I have not been able to satisfactorily demonstrate. Individual variation is one of the difficulties standing in the way of the determination. The dorsal border forms the most distal part of the mid-dorsal line of the limb, and extends to a little below the level of the knee. The ventral border as far as one can judge of it appears to lie not so distally on the mid-ventral line of the limb as does ventral border of the Vth. The most distal part of the mid-ventral line of the limb is therefore occupied by the Vth lumbar field, but the most distal part of the mid-ventral line of the limb is occupied by the VIth lumbar field. This is in harmony with the fact that the ventral edge of the IIIrd lumbar field is the first to leave the mid-ventral line of the trunk and run to a lateral extension of the mid-ventral line on the limb, while the commencement of the mid-dorsal line of the limb is not made until the IVth lumbar segment is reached. A means of testing the correctness of this determination of the borders of the VIth lumbar skin-field lies in delimiting the field and then determining the modification in its area produced by section of the posterior or the anterior half of the root. This I did in three experiments with the results detailed above. The object directly in view was largely frustrated by the great degree of overlap existing between the fields of the anterior and posterior halves of the posterior root. In the experiment in which the filaments composing the anterior half of the nerve-root were severed, the only result detected was an extension of the great notch on the front of the skin somewhat further down toward the ankle; that is to say, the border of the field which embraces the front of the skin certainly retreated some 2 centims. further down the limb. In the earlier of the two experiments on section of the posterior half of the root, the only result obtained was an indubitable diminution of the reflex response over the middle of the back of the ham [illegible] middle of the top of the calf. In the second experiment there was a [illegible] reflex response from the two situations mentioned, and also the [illegible] back of the thigh above the ham indubitably retreated somewhat down the limb. No other alteration were detected although carefully searched for.

In order to discuss satisfactorily the question of the segmental value of the border of the VIth lumbar root, it is here necessary to make a short digression into the action of individual variation upon the limits of the segmental skin-fields belonging to the sensory roots. Regarding the relations of the sensory spinal roots to the skin, it was shown that in *Rana* considerable Individual Variation exists. In *Macacus rhesus* I have shown that as regards the relation of the spinal motor roots to the muscles considerable Individual Variation exists. And this is true also of the sensory roots in *Macacus rhesus.* As shown in a previous paper for the motor roots this Individual Variation is based upon the segmental level of attachment of the nerve fibres to the spinal cord; some individuals possess peripheral motor nerves and muscles *postfixed* at their root attachment to the cord, while in others those structures are *prefixed* at the cord. Similarly in some individuals the cutaneous sensory nerves and skin are *postfixed,* in other *prefixed* as judged by their connection with the spinal roots.

The assertion by VOIGT (8) and KRAUSE (4), that variation only affects the course of nerve fibres, their final distribution at centre and at periphery remaining invariable, was not borne out by my study of the motor fibres, nor do I find it obtain for the fibres of the afferent roots either. If we assume that the nipple is a skin-spot identical in one individual with the nipple of another individual just as it was in a previous paper assumed that a muscle (*e.g.*, flexor brevis hallucis) in one individual is identical with the same muscle in another individual, then the nerve fibres that supply it in one individual do not always supply it in other individuals. The fibres of the IIIrd thoracic root may supply the nipple but sometimes they do not. The skin of the top of the calf is supplied in some individuals by fibres of the VIth lumbar roots, but not in all individuals by the fibres of that root. And this Individual Variation is probably of wide distribution and in minor degrees of extremely frequent occurrence. It affects the accuracy of the lines on the models prepared from my experiments, and could all those lines have been transferred from one individual only they would probably have been more regular than as now represented.

I have shown that, as regards the efferent fibres of the plexus *prefixture* and *postfixture* affect not one anterior root alone, but, usually, a number of anterior roots. In like manner, in the individual in which the field of the VIth lumbar varied from the more usual field in being dislocated from behind forwards, a similar dislocation was evident in the fields of the Xth and IIIrd post-thoracic fields of the individual. Thus, both motor and sensory roots appear within the limitation I have elsewhere mentioned to obey HERRINGHAM'S Law I. (10).

An answer is now possible to a question that has several times occurred to me during the above experimentation. A muscular point is certainly only within limits a fixed point, as regards the spinal segmentation of the body; is a cutaneous point more fixed? In view of the greater age of the posterior root and the superficial position of the skin, it might seem probable that the skin points would be less variable. Judging however from the nipple, the skin of the calf, and of the root of the tail, the fixity of the segmental level of skin points appears no greater than is that of muscular points.

Individual Variation in some ways offers difficulties to the discovery of the arrangement of the segmental skin-fields. But in one way it is advantageous, for it affords further means of assigning to their proper relations the boundaries of a root field. The root-field delimited in an individual possessing an extremely prefixed or postfixed plexus can be compared with the field delimited in individuals of less exceptional plexal construction. I have delimited the field of the VIth lumbar in six individuals, and in one of these the plexus was markedly of a postfixed type. Naturally, the anatomical condition of the plexus was not known at the time of delimitation of the field, nor was the segmental number of the root then known, for it can only be guessed at during the actual operation. Nor, as it happened, was I thoroughly acquainted, at the time of that experiment, with the limits of the VIth lumbar field, for it was only the second experiment on that field that I had made, and I was at that time unacquainted with either the Vth or VIIth lumbar fields. Fortunately, the individual with the delimitation marks on it, and also photographs taken from it, had been preserved. The difference was remarkable. From the specimen it was seen the VIth root of the extremely postfixed plexus was not distributed to the back of the ham and calf, as is the VIth root of the more usual plexus, while it was supplied to more of the front of the leg, especially of the upper peroneal surface than is the case in the more usual plexus. The anterior border lies in the postfixed field more headward (anterior), that is, less distal in the limb; the posterior border lies also more headward (anterior), that is, in the limb more distal, for it is on the posterior side of the limb-apex. If the amount of shifting from the more usual position of the posterior border, by reason of the postfixture, be compared with the amount of the shift of the border produced by section of the posterior half of the root in the two experiments above mentioned, it is found greater in the former than in the latter. The degree of postfixture, therefore, if measured in terms of the rootlets is found to be equivalent to certainly more than one-half of a lumbar segment. As regards the arrangement of efferent fibres in the lumbo-sacral plexus, in none of the species experimentally examined by me did I find the extreme limits of individual variation involve so much as a whole length of origin of one of the larger nerve-roots. The same holds true for my observations on the afferent fibres.

To return; the nature of the distortion of the VIth lumbar field is somewhat as follows. The field is a large one. The dorsal and ventral borders of it are less far [illegible] one another than is the case in the zonal fields on the trunk. The dorsal [illegible] borders are not much enlarged considering the size of the field. The [illegible] and curved, with a short convexity toward the leg, passes fairly directly from the mid-dorsal line of the limb to the mid-ventral line of the limb. Just as in the case of the root-fields on the lower part of the trunk, the field slopes from its dorsal border backwards towards its ventral border. In other words, just as on the lower trunk the ventral extremity of the skin field of the root lies somewhat further from the head end of the body than does the dorsal extremity of the field, so here. And one has seen that the same slant obtains in other root-fields already examined in the limb; but there is a difference between the application of it in the preceding skin fields (*e.g.*, of lumbar IV) and here, because with them the ventral extremity of the field, lying further removed from the head than the dorsal extremity of the field, lay further down the limb than the dorsal extremity; here, with the VIth lumbar root field, the ventral extremity of the field, because it lies further removed from the head than the dorsal extremity, lies higher up, *i.e.*, less distal, in the limb than the dorsal extremity. This is the fuller expression of the fact that was already indicated by the distribution of the Vth lumbar field, viz., that in the limb the essentially zonal root-fields sloping down from mid-dorsal line to mid-ventral line, are now beginning to return from the apical portion of the limb to the proximal. The return procession of the root-fields from the apex of the limb to the trunk, commences with the VIth lumbar skin-field, just as the outward procession of the root-fields from the trunk to the limb apex commences with the Ist lumbar field. And the distortion of the root-field by the excrescence of the limb, instead of affecting the posterior edge of it more greatly than the anterior (IInd, IIIrd, IVth, and Vth), now implicates the anterior edge more deeply than the posterior. Further, this VIth lumbar root-field besides being distorted has been dislocated from the side of the trunk to the extremity of the limb, or, in other words, from the middle or primary axial lines of the trunk to the distal end of the secondary axial lines, the middle lines of the limb.

The skin-field of the VIIth post-thoracic root extends over almost the whole of one aspect of the limb, as a long strip. It is, therefore, a large root-field, but it appears at first sight not so obviously distorted from the simple zonal type as are the previously described root-fields of the limb. Its dorsal and its ventral border are not extensive, considering the size of the field; they lie a much less distance apart than do the distance separating the dorsal and ventral borders of the cutaneous root-fields on the trunk. The anterior border of the field sweeps from the mid-dorsal line of the limb at a point somewhat above halfway between the knee and hip. From that point it descends over the outer hamstring and the outer head of the gastrocnemius to enter the dorsal aspect of the foot in front of the external malleolus, and passes usually to the medial side of the third digit on to the sole. On the sole it usually runs along the prominence caused by the short muscles of the hallux to reach the groove behind the internal malleolus, and thence runs up the leg on the inner head of the gastrocnemius, finally sloping into the mid-ventral line of the limb about one-third up the thigh. The posterior border is very much shorter than the anterior (about 15 centims. as compared with 47 centims.). It passes from the mid-dorsal line of the limb a little above the hip, backwards round across the gluteal region outside the ischial callosity, to reach the mid-ventral line of the limb at the top of the thigh.

The distortion of the original simple zonal-shaped field into this figure has affected chiefly its anterior border; that border has been prolonged as a long narrow tongue thrust down the whole length of the thigh, leg, and foot, and containing the skin of the three outer digits at least. It is thus clear that the apparent resemblance of the VIIth post-thoracic skin-field to the original simple zonal root-field is of superficial character; so great is the distortion that has really occurred that what was originally the long diameter of the strip has become the short diameter, and the long strip figure of the field is caused by the development of a huge spur from the anterior edge of it.

The VIIIth post-thoracic root-field is more easily explained in reference to the relation of its borders to those of the original simple zonal field. The dorsal and ventral borders of it coincide with the mid-dorsal and mid-ventral lines of the limb, and apparently are of considerable length. The distance that separates them is about one-half the circumference of the limb. The posterior border is shorter than the anterior, as in the case of two preceding root-fields. It starts from the mid-dorsal line of the limb somewhat proximal to the point at which the VIIth root-field in my specimens started, and sweeping down over the buttock passes internal to the ischial callosity and appears in front at the side of the pubes, meeting the mid-ventral line of the limb in the most proximal part of that line. The direction of the anterior border near its junction with the mid-dorsal line of the limb is so similar to that of the mid-dorsal line itself that it is difficult to locate exactly. It seems to lie somewhere below half-way between the hip and the knee. It descends, and then ascends, enclosing a tongue-shaped flap of variable length and size upon the back of the calf; its place of junction with the crural mid-venter is difficult to determine, for the same reason as renders difficult the determination of the junction of the border with the mid-dorsal line of the limb.

The nature of the distortion undergone by the VIIIth post-thoracic skin-field in the excrescence of the limb appears to affect chiefly the anterior part of its field. A flap has protruded forward from it (that is to say *down* the limb), and the width of the base of the flap is so great as to involve the whole anterior border from mid-dorsal line of the limb to mid-ventral line of the limb. As in the case of the preceding roots the end of the tongue-shaped flap is situate about half-way between the mid-dorsal and mid-ventral lines, so that the skin of the middle line of the top of the calf and ham, like the skin of the digits, corresponds with the skin of the mid-lateral aspect of the trunk (the region of the *mid-lateral line*). *V. supra*, p. 691.

The nature of the distortion of the IXth post-thoracic root-field has been already explained. The root-fields behind it treat the middle line of the perinæum and the [illegible] under surface of the tail as the mid-ventral line of the body, [illegible] and anus are openings in the ventral aspect of the body, [illegible] the posterior pole.

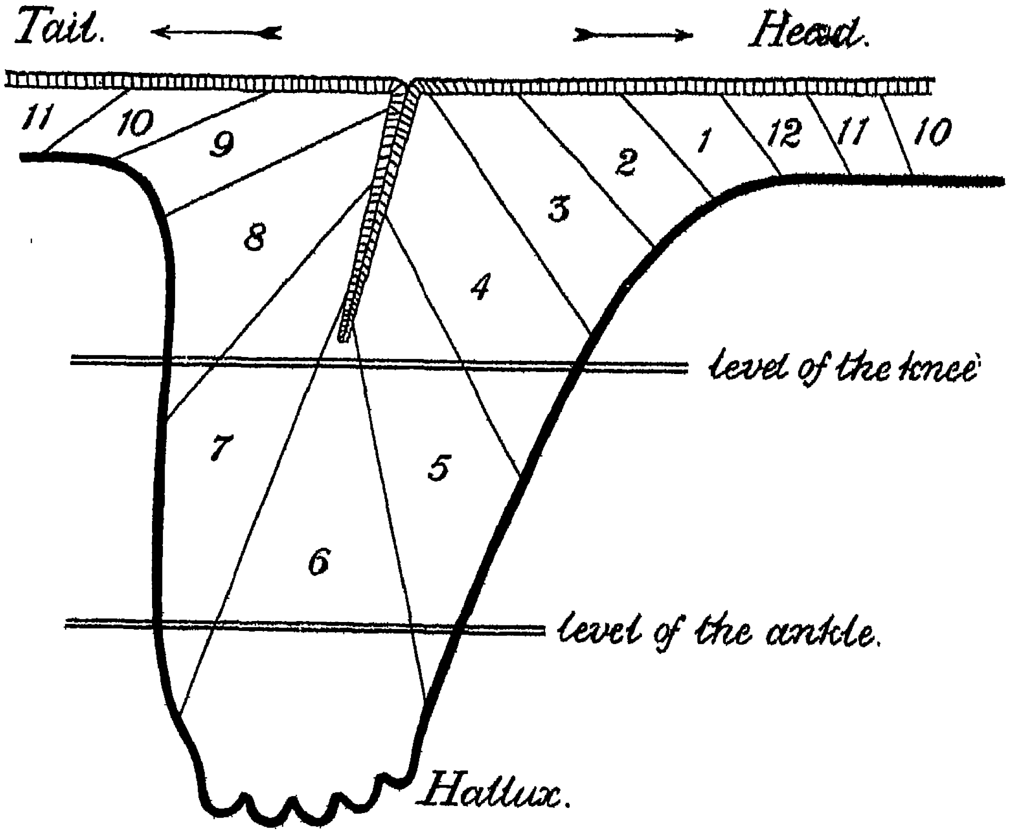
On comparing the segmental arrangement of the skin of the limb with that of the musculature of the limb, a difference becomes evident between them that is true of the fore limb as well as of the hind. I have in a previous paper shown that the limb, as regards its musculature, is composed of rays extending at right angles to the long axis of the trunk, and arranged in fore-and-aft series in such a way that the pelvic limb has a sloping anterior edge, into the composition of which enter four rays, each extending further into the limb than the ray preceding it. The posterior edge of the limb is abrupt and composed in its whole length by one ray only, the 6th, or most posterior of those which contribute to the limb musculature at all. The 5th ray like the 6th extends from the base to the free apex of the limb. A similar scheme of structure for the anterior limb is evidenced by the root supply to the musculature of it; there also the posterior border of the limb is not formed by segments extending stepwise down into it, but is abrupt and formed by the ray of the IInd thoracic segment. With this arrangement of the musculature the segmentation of the skin of the limb does not correspond. In the skin of the limb the posterior border, like the anterior border, is constituted by a series of overlapping segments and not by a single segment; and this is true of both anterior and posterior limbs alike. The segmental arrangement of skin and musculature is also different in another respect.

The motor spinal roots supplying the muscles of the limb, even those roots which penetrate farthest into the limb, all of them contribute still to the supply of the muscles of the trunk. That is to say, the segments of the limb musculature are not detached from the mid-axis of the trunk. The 5th muscular ray of the pelvic limb which contributes to the musculature of the limb in even the free apex of the limb never loses its base in the axial muscles of the trunk, and gives a share to such axial trunk muscles as the sacro-coccygeus. So also does the 6th ray.

On the other hand, at the surface of the limb the segments of the skin seem to be actually dislocated from their attachment to the dorsal and ventral axes of the trunk; they appear to be detached from the mid-dorsal and mid-ventral lines of the body. Into the base of the limb the mid-dorsal line of the body thrusts sidewise a branch, a secondary lateral axis, almost at right angles to its own direction. The mid-ventral line behaves in a like manner. These are the *mid-dorsal* and *mid-ventral lines of the limb.* Upon these secondary dorsal and ventral axes the cutaneous segments of the limb are ranged, as though upon folded portions of the axial lines of the trunk itself. It must be remembered the distribution revealed in the cutaneous fields is probably an arrangement literally *only skin deep.* The difference between the arrangement shown for the motor root and that for the sensory root may be really *less* due to the comparison being of *efferent* with *afferent* distribution, than to the comparison being of *muscle* with *skin.* From such glimpses as I have occasionally obtained of afferent fibres from muscles (*e.g.*, afferents for knee jerk, afferents of antagonistics of "jerk" muscles), these afferent fibres seem to belong strictly to the same segments as supply motor fibres to their muscles

It is interesting to note that no cutaneous branches can be found by dissection to be given from the posterior primary divisions of the Vth and VIth post-thoracic nerves of *Macacus rhesus*—at least, I have failed to find any. The muscles of the back do receive branches from the posterior primary divisions of these nerves, and in the musculature of the back the nerves end. SWAN* says of the IVth and Vth lumbar nerves of Man that the posterior primary divisions of them give off no cutaneous branches. The same is true of the VIIth, VIIIth, and sometimes VIth cervical nerves. TÜRCK (7) says that in the Dog the IVth, Vth, VIth, and VIIth lumbar nerves yield no supply to skin by their posterior primary divisions. This apparent absence of cutaneous distribution by the posterior primary divisions of these nerves is, I would suggest, a sign that they are at the very centre of the limb region —the region in which the skin segments have slipped outward down the limb. It is a point which apparently escaped ROSS (14), and is unrecognised in his suggestive essay mentioned above.

Fig. 8.



Scheme of the sensory Spinal skin-fields of the hind limb of *Macacus rhesus*. The overlapping is not indicated.

In *Macacus rhesus* to the cutaneous surface of the anterior aspect of the hind limb six segments contribute, the Ist, IInd, IIIrd, IVth, Vth, and VIth post-thoracic, to that of the posterior aspect four segments, the VIth, VIIth, VIIIth, and IXth post-thoracic; to the cutaneous surface of the posterior aspect of the fore limb five segments contribute, the Vth, IVth, IIIrd, IInd, and Ist thoracic; to that of the anterior aspect of the limb six segments contribute, the IIIrd, IVth, Vth, VIth,

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* JOSEPH SWAN, "Demonstration of the Nerves." London, 1834.

VIIth, and VIIIth cervical. There is thus a curious agreement in the number of segments contributing to the surfaces of the fore and hind limbs. And in each the anterior aspect is seen to be segmentally more extensive than the posterior, just as was found to be the case with the musculature of it.

The number of segments contributing to the skin of the limb is seen to be greater than the number of segments contributing to its musculature. From examination of the motor fibres of the lumbo-sacral plexus, it was concluded that the limb, "plastic, like the rest of the body, has been moulded by variation and by function, but not so rudely as to seriously obscure its segmental plan." The segmentation at the surface of the limb presents, as has just been shown, certain characters different from the segmentation of the deeper parts. From examination of the segmentation of the skeletal muscle of the limb, it was concluded that "the quadrifid or quinquifid digital partition of the free end of the limb does not imply that respectively four or five segments are prolonged into the apex of the limb."*

In like manner, with the cutaneous segmentation of the limb, the quadrifid or quinquifid digital partition at the end of the limb has nothing to do. The skin of the four pedal digits of the Cat belong to three of the cutaneous segments in common (VIth, VIIth, VIIIth post-thoracic). The skin of the five pedal digits of *Macacus* belong to three of the cutaneous segments in common (the Vth, VIth, VIIth lumbar). I have shown elsewhere and in the present paper that the 5th segment of *Macacus* is the 6th of Cat. The skin of the hallux, therefore, of *Macacus* is produced by an extension of the skin of the segment, which is the 6th in the Cat, and is formed by the excrescence of another digit from a segment already bearing digits, and not by the introduction of another segment into the foot.

In describing experiments on the motor fibres to the muscles of the foot and hand, I have mentioned that it is extremely difficult to get any evidence that the intrinsic musculature of the 1st digit is segmentally anterior to the intrinsic musculature of the 5th digit.† But the evidence that the skin of the 1st digit is segmentally anterior to the skin of the 5th digit is from the above experiments definite enough; the skin of hallux is shown to be segmentally anterior to skin of secundus, that of secundus to that of tertius, and so on; the skin of the dorsum of the foot is shown to be segmentally anterior to the skin of the plantar aspect.

W. KRAUSE (4) has stated that in the Monkey and Rabbit the absolutely longest fibres in the brachial nerves are those of the VIIIth cervical, which pass to the end of the 3rd digit of the hand, and SCHWALBE‡ has based his inferences regarding the size of the nerve-fibres partly upon KRAUSE's statement.

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* SHERRINGTON, *loc. cit.*, p. 767.

† 'Journ. of Physiol.,' vol. 13, p. 744. (Professor PATERSON tells me he has by dissection succeeded in the human subject in demonstrating this interesting point by unravelling the root-components in the muscular nerves.—July, 1893.)

‡ 'Handb. der Neurologie.'

In judging these inferences it is well to remember that the Ist thoracic root also contains fibres for the tip of the digit, and that the inferences should also be applicable to the fibres of the VIth and VIIth post-thoracic nerve-roots, which in *Macacus* contains the longest nerve-fibres in the whole body.

Using the segments of the skin as a guide, it is interesting to note how clearly they demonstrate that the situation of the anus is not at the posterior pole of the body, but that it belongs distinctly to the ventral aspect of the body.

The umbilicus is placed about midway between the anterior and posterior borders of the XIth thoracic root field.

The field of the XIIth thoracic root-field also includes it, the anterior border of that field lying distinctly above the umbilicus. The Xth thoracic root-field came near to it, but did not actually include it in my delimitations.

The nipple lies about midway between the anterior and posterior borders of the IVth thoracic root field; it is also included by the Vth thoracic root-field, and partly (probably entirely) by IIIrd thoracic root-field also.

The edge of the vulva lies in the IXth post-thoracic root-field; the anterior, or lower portion of the edge, and the side of the clitoris, is included in the VIIIth post-thoracic root-field as well; the posterior, or upper portion of the edge, is included in the Xth post-thoracic root-field, as well as lying well within the field of IXth root.

The anus is in the Xth post-thoracic root-field, and is included also especially at its ventral edge in the IXth post-thoracic root-field.

The scrotum and side of the penis form part of the cutaneous field of the IXth post-thoracic root. The front of the scrotum and the skin of the penis are also included in the VIIIth post-thoracic skin-field. The posterior part of the scrotum is included in the Xth post-thoracic skin-field.

The skin of the hallux is part of the VIth post-thoracic root-field, and is included also in the Vth post-thoracic root-field.

The skin of the 3rd, 4th, and 5th digits is part of the VIth post-thoracic root-field, and is included as in the VIIth post-thoracic root-field.

The Genital Flap.—In the female the skin fields of the VIIIth and IXth post-thoracic sensory roots come forward under the symphysis pubis to appear on the front of the pubic region making, right and left areas together, a low triangular field with an obtuse angle above, and the base of the figure below on two slightly prominent folds at the top of the inner border of the thigh-folds, which may be called the genital folds. This ventral extension of these sacral skin-fields may be called "the genital flap." It is a flap that has been delimited by disease or injury in man, and is figured more than once in THORBURN'S 'Surgery of the Spinal Cord.' It is also described by STARR (18), J. MACKENZIE (19), and HEAD (20). The genital flap is larger in the male than in the female Macacque, it includes the scrotum and the penis to its root. At its edge the IInd and VIIIth post-thoracic sensory skin-fields seem to meet and slightly interlap. In the male Cat it comes still more forward over the pubes, and resembles the configuration given for it in the Dog in one of the sketches left by TÜRCK (7).

PEYER (2) from his experiments on the fore limb of the Rabbit, advanced the statement that the skin overlying a muscle in the limb is supplied with sensory nerve-fibres by the same spinal nerve which contributes motor fibres to the underlying muscle. This conclusion was reaffirmed by W. KRAUSE (4). It harmonises with a "law" previously formulated by SCHRÖDER VAN DER KOLK,* that the sensory branches of a nerve that gives off motor branches always pass to that part of the joint which is moved by the muscles which the motor branches supply. V. DER KOLK's law had reference chiefly to the distribution of the nerve trunks of limb-plexuses, and was not, by V. DER KOLK, applied to the distribution of pure spinal nerves. That in the trunk the skin overlying a muscle is supplied with sensation by the same spinal nerve as that supplying the motor innervation to the muscle is no doubt generally the case. But a fact of greater constancy is that between the anterior and posterior borders of the skin-field of a posterior root, the mid-point lies posterior to the mid-point of the muscular field of the anterior root. The cutaneous field of the sensory root lies somewhat further back than does the muscular field of the motor root. And this obliquity of mutual relationship becomes greater as the trunk is followed backwards. The cutaneous field of the VIIth thoracic sensory root covers the whole of the 7th intercostal space, and more or less of other intercostal spaces also. The skin-field of the Xth thoracic root overlies a small portion only of the 10th intercostal space, but largely the 11th space, and the 12th rib. The skin-field of the sensory root of the XIIth thoracic does not overlie its corresponding rib at all, but is altogether behind it. The skin-field of the IInd lumbar sensory root extends some distance down the front of the thigh; the motor root of that nerve innervates muscles which at lowest extend as far as the trochanter minor of the femur. The skin field of the IIIrd lumbar sensory root extends as far as the lower end of the femur; the distribution of the fibres of the motor root extends no further downwards than the upper part of the thigh. For the IVth lumbar nerve the skin field of the sensory root extends to half way down between the knee and ankle; the distribution of its motor root in no instance descends below the knee. In the Vth lumbar nerve the skin field of the sensory root descends to the tip of the 1st digit; the distribution of its motor root in no instance reaches the muscular fibres of the foot. As an outcome of the graduated descent of the limb by the spinal skin-fields, followed by their ascent on its segmentally posterior aspect (described above), when the VIIIth post-thoracic segment is reached the skin-field is found, instead of extending farther down the limb than the motor supply, to extend less far down; the former stopping short at the calf of the leg, the latter running down into the intrinsic muscles of the foot.

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* FRORIEP's 'Notizen,' 3rd Series, iv., 129 (1847).

The maximum discrepancy in the limb between the locality of distribution of the afferent and efferent portions of the same segmental nerve seems attained with the IXth post-thoracic (Cat) and IInd thoracic (Monkey). The motor fibres of these nerves descend to the intrinsic musculature of the foot. The skin-fields of the corresponding sensory fibres lie much nearer the base of the limb, *i.e.*, posterior to the muscular field.

So, also, with the upper thoracic nerves, the discrepancy between the locality of motor, muscular, and cutaneous sensory distribution is very marked. In the case of the IInd thoracic nerve, the motor root reaches the intrinsic muscles of the hand; the sensory root does not supply the skin even so far down as the wrist. In the case of the IIIrd thoracic nerve, the motor root does not supply any of the muscles of the limb proper, but the sensory root supplies the skin of the arm as far as the elbow. In the IVth thoracic nerve, the motor root does not supply any of the muscles of the limb proper, but the sensory root supplies part of the skin upon the upper arm.

An exception of less value, and probably different significance, is instanced by the portion of the cremaster attached to the testis in the scrotum. The cremaster belongs to the IInd and IIIrd, less commonly to the IVth lumbar segments. The scrotal skin overlying it belongs to nerve-roots five segments lower down, viz., to the VIIIth and IXth post-thoracic (the Ist and IInd sacral of *Macacus*).

This leads one to remember that the anterior and posterior roots of the spinal nerves are not, when traced downwards to their correlatives in the simplest forms of the vertebrate phylum, placed at the same segmental level. In the Cyclostomata and the Selachians, as well as in some Ganoids, the posterior and anterior roots are placed alternately. I have not been able to find whether there is evidence of such alternate distribution at the time of their first origin in the Mammalian embryo. The posterior root appears to be of older structure. SCHWALBE remarks: "Es würden also die *dorsalen* Wurzeln sammt ihren Ganglien für die Beurtheilung der Segmentirung des Nervensystems von grosser Wichtigkeit sein."*

A practical outcome of the above arrangement is that especially in the lower half of the trunk, and in the anterior surface of the limb, the skin of any point will be supplied with sensory nerves from spinal roots segmentally anterior to the spinal roots whence come the motor nerves to the underlying muscle. A partial exception to this is the skin of the back of the thigh, where, owing to the re-ascent of the limb by the skin fields the supply of both skin and subjacent muscle may be from the same segmental level.

Difficulties have been encountered by the surgeon from the want of recognition of this rule.† If, for example, in a case of paraplegia, the lower level of the field of æsthesia lie at the lower border of the 11th rib, it must not be supposed that the

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* 'Nervenlehre,' p. 808.

† For a surgical instance actually applying this to the case of Man, see 'Med.-Chir. Trans.,' vol. 71, [illegible] 'Diseases of the Nervous System,' vol. 1, p. 559, 2nd Edition.

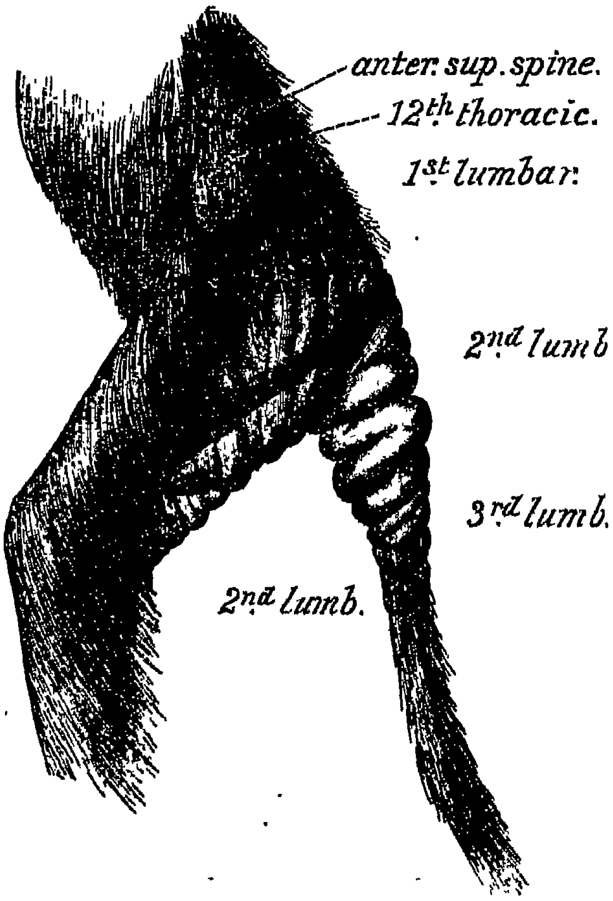
interruption of the spinal cord is situate below the origin of the XIth spinal nerve; the interruption in *Macacus* would lie under the origin of the IXth spinal nerve, or, as the above experimental fields are minimal, more probably under the origin of the VIIIth spinal nerve, that is to say, three segments higher up, and the discrepancy will be greater at the 12th rib than at the 11th, and it will be greater at the vertebral end of the rib than at the costal, for there the lower border of the 12th rib will correspond with the lower (posterior) edge of the VIIth thoracic root-field.

It is clear from the above that if coincidence of locality of nerve distribution in muscle and skin be taken as the rule, it must be applied circumspectly. The skin-field extends beyond the muscular field in a posterior direction, sometimes in an anterior direction also: VAN DER KOLK'S "law" (HILTON'S "law") is true in many places, partly by reason of its indefiniteness, a single muscular group usually causing movement at more than a single joint; partly because in regions in which the joint moved by a muscle lies segmentally posterior to the place of origin of the muscle, it will apply as the inevitable result of the above more fundamental rule of relation between overlying skin and underlying muscle. But in other parts, such as the flexor aspects of the thigh and leg and extensor aspects of the arm, it does not hold true, because there contrary to the segmental disposition of the parts. This so-called law, therefore, although imbued especially by HILTON with a teleological significance, is really a phenomenon due to the segmental arrangement of the body and possesses metameric rather than functional significance.

It must be remembered that the sensory fields delimited in the present research are cutaneous, and literally skin deep only. In such glimpses as we obtain of the distribution of sensory nerve-fibres to muscles they seem to correspond segmentally with the motor supply. To this I shall return in a subsequent paper.

By means of the pilomotor nerves it is possible to delimit in many cases fields of cutaneous distribution of the anterior root and of the sympathetic ganglion. It is interesting to inquire how far these cutaneous fields of the motor roots correspond with the cutaneous fields of the sensory root. This question may be examined in the fields of the third thoracic and highest three lumbar nerves of *Macacus rhesus*. The root territories there do not correspond. The want of correspondence is in these roots very marked indeed, so that it may happen that the cutaneous field of the one at no point coincides with the cutaneous field of the other. The pilomotor fibres of the IInd lumbar are distributed to the posterior part of the hip, buttock, upper thigh, and tail, over an area other than the cutaneous field of the IInd lumbar sensory root. The pilomotor field of the IIIrd lumbar (a field not constantly demonstrable in my experiments) lies as above and nearer the root of the tail; a region other than the skin field of the afferent root of the same segment. The pilomotor fibres in the anterior root of the IIIrd thoracic erect the hairs on the front of the scalp, but the skin field of the sensory root of that nerve is a zonal strip over the scapular and mammary regions of the chest extending down the side of the arm. As to the correspondence of the pilomotor fields of the ganglia with the skin fields of the sensory spinal roots, it was shown in a paper by LANGLEY and myself that the pilomotor fields of the sympathetic ganglia are but slightly overlapping fields. Now the overlapping of the cutaneous fields of the sensory spinal roots is one of their most characteristic features. The fields of the two cannot therefore exactly coincide, but they seem to correspond in locality though not in extent.

Fig. 9.



Area of sexual skin in a young female, *M. rhesus.*

I have looked with some interest to see whether a similarity exists between the patterns of the skin-markings of animals and the segmentation evidenced in the above experiments. Among the Monkeys commonly obtainable in this country skin-markings are largely confined to the face and buttock. Regarding the skin on the buttock of the Monkey I shall mention an observation later.

The stripes on the back and sides of the Tigor present a general correspondence with the segmental arrangement of the skin in that part, but all the structures of the body are there so segmentally arranged that it is only possible to say that the surface-markings follow the direction of the rest of the segmentation. On the buttock and thigh the direction of the skin-marks does follow the arrangement of the sensory root fields in a general kind of way, but without detailed correspondence except in the following particular. The existence of what I have called the mid-dorsal line of the limb is plainly recognizable by the skin-markings. The stripes start from and meet on a line which, in position and length, corresponds with the mid-dorsal line of the limb described above. Below the knee the striping largely fails, and such as is present tends round the leg in a ring-like fashion. The correspondence there is wanting.

The skin stripes of the Zebra follow the segmental arrangement on the trunk and neck, and exhibit the peculiarity of being boldly continuous across the mid-dorsal line. It is therefore interesting that the arrangement of the cutaneous stripes on the haunch differs from that of the Tiger in also passing boldly across the haunch, that is to say, bears the same relation to the mid-dorsal line of the limb as on the trunk and neck do the stripes there to the mid-dorsal line of the body. The stripe on the shoulder of the Ass corresponds with the mid-dorsal line of the fore-limb.

After from experiment becoming acquainted with the limits of the cutaneous fields of the VIIIth, IXth, and Xth post-thoracic roots, I was, on observing a female specimen older than most of those I had worked with, struck by the close resemblance between the shape of the region of semi-erectile skin on the limb which flushes during the menstrual period (fig. 9) and that of the combined areas of the VIIIth, IXth, and Xth nerves. The correspondence appears curiously accurate, and I would suggest that the pattern of this region of sexual skin is segmental, and connected with the relation of VIIIth IXth and Xth post-thoracic sympathetic ganglia to the skin, and of the VIIIth IXth and Xth post-thoracic roots to the sexual organs.* It is true that in the fully mature females the area of sexual skin seems to vary somewhat in extent. I have seen it descend the calf to the outer edge of the tendo Achillis above the heel; but this is to my mind no argument against, but rather one for, the connection I suggest, as though I have met no instance, I cannot but think that when the plexus is postfixed the skin above the heel may be included in the region of the VIIIth root. I should imagine that it would have been found to do so in the very postfixed specimen of which the VIth post-thoracic skin-field was determined. The photographs of the specimen almost prove that in it the VIIIth post-thoracic skin-field did descend to behind the outer malleolus, because that skin is not included in the VIth root, and therefore, to possess a double root supply as the skin of the limb everywhere does, must have received the filaments of the VIIIth as well as the VIIth. If this explanation of the position and figure of this area of sexual flushing is correct, the phenomenon would fall into the same category as the association of the distribution of somatic pain to the distribution of splanchnic sensory irritation, as sketched by Ross in his essay (16), and further developed by J. MACKENZIE (19) and by HEAD (20).

If the above flushing really be, as suggested, of visceral and reflex origin, it suggests the existence of vasomotor nerves to the skin in question from the VIIIth and IXth roots, the hind limb would obtain vasomotor nerves from two regions of the spinal cord, the lower thoracic, and upper lumbar roots as determined by ROSE BRADFORD and BAYLISS,† and from the sacral roots as well. I am not sure that this sexual flushing is confined to the female Macacque, but it is more marked in her than in the male. Mr. HEAPE, a high authority on the subject, writes to me that some males show it well.

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* See note on p. 761.

† ARRIS and GALE Lecture, 1892. *Cf.* also OSTROUMOFF, 'PFLÜGER'S Archiv,' vol. 12, p. 261.

This communication is unfortunately long. It seems therefore desirable to again epitomize some of the main results of the experiments as a conclusion.

Although in a plexus each posterior spinal root gives separate contributions to several nerve-trunks, the cutaneous distribution of the root is composed not of patches which are disjoined but of patches which are so joined that the distribution of the entire root forms one continuous field. Similarity of the root composition of neighbouring nerve-twigs that are near their destination is a necessity of this arrangement. Thus the dorsal collateral digital nerve on the tibial side of a digit will resemble in root composition the plantar collateral digital on the tibial side of the same digit, although they are derived from separate parent trunks. The dorsal digital nerve entering the cleft between the first and second toes, is interpolated in the digitals from the musculo-cutaneous trunk, although it comes itself from the anterior tibial trunk. Yet by its root composition it falls into perfect series with that of the other digital nerves.

The field of skin belonging to each sensory spinal root may be called the *sensory spinal skin-field* These fields are segmentally arranged and do not present the same variety of configuration presented by the fields of peripheral nerves. In each spinal field reflex reaction is less easily elicitable near the edge of the field than the field elsewhere.

Each sensory spinal skin-field extends to a certain extent across the neighbour skin-fields. Each has an *anterior overlap* extending into segmental fields anterior to it, each a *posterior overlap* into fields posterior; each has also *crossed overlaps* trespassing into the fellow field of the opposite lateral half of the body, both at the mid-dorsal (the *dorsal crossed overlap*), and at the mid-ventral line (the *ventral crossed overlap*). The fore and aft overlaps are throughout the body very great, and it appears that each point of skin throughout the body is supplied by at least two sensory spinal roots, in certain regions by three. The overlap of the skin-fields of the separate filaments of a posterior root is very great indeed, at least in some cases.

The shape of a sensory spinal skin-field is, where simplest, *e.g.*, in the trunk and neck, a band, wrapped transversely round one lateral half of the body with fairly parallel borders, but somewhat wider near its ventral than at its dorsal end. In the limb the segmental skin-fields are distorted from the simple band-form. The distortion of each segmental field in the hind limb and of some in the fore limb is in the foregoing papers analysed, and for each the true anterior border, the true posterior border, and the true dorsal and ventral borders are found. This analysis is only possible after it has been recognized that in the limb the cutaneous segments are not only distorted but are seemingly dislocated from the primitive position of attachment to the mid-dorsal and mid-ventral lines of the trunk. The mid-dorsal line of the body may be said, in the region of the limb, to extend outwards as a side branch, a secondary axis, almost at right angles to the rest of itself. Similarly in the same region the mid-ventral line. Upon these dorsal and ventral side-lines, as upon secondary dorsal and ventral axes, the cutaneous segments of the limb are ranged, as though upon folded portions of the axial line of the trunk itself. The position of these secondary axes having once been found (as described above, pp. 743, 749) in the limb, it is not difficult to examine the degree of dislocation and distortion undergone by each segmental field.

In the segmentally anterior aspect of the limb each segmental field has been curved so as to present a very convex posterior edge, and the posterior *overlap* of the field is very large. In the segmentally posterior aspect of the limb each segmental field has been curved so as to present a very convex anterior edge, and the anterior *overlap* of the field is very large. The dorsal and ventral borders of the fields are, in the limb, not much increased in length.

Owing to their serial arrangement along the mid-dorsal and mid-ventral lines of the limb, there is an axial crossed overlap of the fields there of such a kind that a segmental field may there crosslap with a segmental field far removed from it in the segmental series, *e.g.*, IXth post-thoracic with IVth post-thoracic.

The dislocation of certain of the segmental fields in the limb so as to lie parted from mid-dorsal and mid-ventral lines of the body is apparent rather than fundamental in character; it is wanting even in the pelvic limb of *Rana.*

The absolute segmental level of a point of surface is subject to Individual Variation, just as that of muscular points in the body-wall and viscera. This Individual Variation affecting the skin is correlated with variation in the constitution of the afferent spinal roots, so that the limb plexus may be *postfixed* or *prefixed* by its sensory roots just as it may be by its motor roots. A mixed nerve may be postfixed by its motor roots and by its sensory roots in the same individual, or may be prefixed by both. There is some evidence (Frog) that a plexus may be prefixed by its motor roots when it is not so by its sensory roots, and *vice versâ.*

Position on the limb of the *axial lines* of the limb (Plate 51, fig. 19):—

Upon each limb exists a *mid-dorsal line* and a *mid-ventral line* branching from the *mid-dorsal* and *mid-ventral lines of the body* and almost at right angles to those latter. The axial lines for the hind limb slope outward from the middle lines of the body somewhat backward as well as outward; those for the fore limb conversely slope somewhat forward as well as outward. The *mid-dorsal line* in the hind limb runs from the mid-dorsal line of the body over the sacrum past the back of the hip joint, and along the outer face of the thigh nearly to the knee. Of the *mid-dorsal line* of the fore limb only the most proximal part is described by the present experiments; that part runs from the mid-dorsal line of the body outwards and forwards over the infraspinous scapular fossa. The *mid-ventral line* of the hind limb runs from the front of the body of the pubes to the inner border of the thigh and descends on the gracilis fold nearly to the knee. The *mid-ventral line* of the fore limb is, in the present experiments, only followed for its proximal part; that part lies on the chest close below the clavicle.

Using the cutaneous fields as a guide to the morphological position of various points in the body, it is seen that the edges of the foot and hand with their digits lie in the spinal skin-fields of the limb about midway between the mid-dorsal and mid-ventral lines, and therefore correspond with the *mid-lateral line* of the trunk (p. 691). The digits are therefore buds from the region of the *mid-lateral line*, and the preaxial and postaxial borders of the limb lie also in the mid-lateral line of the body.

From the motor roots it is not easy to get evidence that the 1st digits of the foot or hand is segmentally anterior to the 5th digit; the root supply of the intrinsic musculature of each is so similar. But from the sensory roots it is easy to show that the skin of the 1st digit is segmentally anterior to that of the 2nd digit, that of the 2nd to that of the 3rd, and so on. The skin of the dorsum of the foot is shown to be segmentally somewhat anterior to the sole.

The number of segments entering into the composition of the skin of the limb is seen to be greater than the number of segments contributing to its musculature. To the anterior aspect of the fore limb six segments contribute (IIIrd, IVth, Vth, VIth, VIIth, VIIIth cervical); to that of the hind limb six segments also (Ist, IInd, IIIrd, IVth, Vth, and VIth post-thoracic). To the posterior aspect of the fore limb four segments contribute (Ist, IInd, IIIrd, IVth thoracic); to that of the hind limb four segments also (VIth, VIIth, VIIIth, IXth post-thoracic).

In each limb the preaxial border is segmentally more extensive than the postaxial. I have shown that this last fact is exemplified even more strikingly in the musculature of the limb, both fore limb and hind limb.

The quadrifid or quinquifid digital partition of the free end of the limb is no indication of the number of segmental skin fields in the limb.

The distribution of the fibres of the sensory spinal root in the limb, as elsewhere, indicates a segmental significance in their constitution rather than a functional based on co-ordination. Without denying the existence of functional factors in the progressive development of the limb, it must be admitted that there is little evidence that the collection of fibres in each sensory root has resulted from an assortment of the fibres with a view to assisting toward functional co-ordination.

PEYER's statement of the identity of the muscular and cutaneous distributions of a spinal nerve does not bear minute examination. The IInd thoracic nerve may innervate the intrinsic muscles of the hand, but its skin-field does not reach the hand at all. In the lower half of the trunk and in the pelvic limb, the skin at any point tends to be supplied by sensory spinal roots segmentally anterior to (higher than) the spinal motor roots supplying the subjacent muscle. A partial exception to this will be in the skin of the back of the thigh, where, for reasons above explained, the supply of both tends to be from more truly parallel segmental levels.

The cutaneous fields of the sensory spinal roots do not correspond closely with the fields of distribution of the motor roots in the skeletal muscles, nor do they correspond with the fields of cutaneous distribution of the motor roots as judged of by the pilomotor fibres of those roots, but the pilomotor fields of the sympathetic ganglia and the cutaneous sensory fields do correspond.

In *Macacus rhesus* there seems a close topographical correspondence between the area of sexual skin at the root of the tail, on the buttock, and along the back of the thigh and the combined sensory skin-field of Xth, IXth, and VIIIth post-thoracic roots.

I wish in concluding to mention my indebtedness to Professor MICHAEL FOSTER for opportunities and counsel freely given upon several occasions. I would also thank my friends Dr. ROSE BRADFORD and Dr. HENRY HEAD, the former for largely suggesting the research, the latter for instituting comparison between the experimental areas dealt with in this paper and his own extended clinical observations of a somewhat converse nature. [To Professor PATERSON and to Dr. JAMES MACKENZIE I am very greatly indebted for criticism afforded when these pages were passing through the press. Two diagrams, on Plate 52, were kindly sketched for me by Professor PATERSON.]

[NOTE.—June 12, 1893. LANGLEY's observations on the sympathetic system lead him to conclude that the cutaneous distribution of the pilomotor and secretory fibres arising in a sympathetic ganglion is the same as the cutaneous distribution of the sensory fibres arising in the corresponding spinal ganglion.* In testing the point, he suggests for comparison with the sensory skin-fields of the limb the secretory nerves (post-ganglionic) of certain ventral cutaneous branches running to the hind foot. I had tentatively delimited the skin-fields for the hind limb of the Cat some time since when examining the account given of the Dog by TÜRCK. After reading Mr. LANGLEY's paper I have repeated the experiments with special attention to his point, using, as before, the method in Experimental Series No. II. In the *pad* and *cushions* of the hind paw the fields of the VIth, VIIth, and VIIIth post-thoracic spinal ganglia were compared with the fields of the corresponding sympathetic ganglia as revealed by post-ganglionic sweat-fibres, and figured in LANGLEY's paper. The agreement of the fields was found to be close; it may be exact, but the sensory fields as actually delimited were rather less extensive than the sweat fields figured. Once only in five experiments was a contribution from the IXth post-thoracic sensory root detected; where it existed the contribution closely agreed with the corresponding sweat field figured by LANGLEY. The results accord, therefore, with LANGLEY's conclusion, which, sufficiently interesting in itself, is the more important as from it he proceeds to further generalisation.—C. S. S.]

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* 'Journ. of Physiology,' vol. 12, p. 347; 'Roy. Soc. Proc.,' vol. 52, p. 547.

EXPLANATION OF PLATES 42–52.

In Plates 42, 43, 44, 45, and 46 the *field of response* (see pp. 649 and 688) is limited by a double line of white and black; the white side of the line lies toward the *field of response*, the black toward the surface whence no response was elicited.

PLATE 42.

Fig. 1. The IInd thoracic field, with posterior edge of IVth cervical, and anterior edge of VIIth thoracic.

Fig. 2. The IIIrd thoracic field, with posterior edge of IIIrd cervical, and anterior edge of VIIth thoracic.

PLATE 43.

Fig. 3. The IVth thoracic field, with posterior edge of IIIrd cervical, and anterior edge of VIIth thoracic.

Fig. 4. The VIIth thoracic field, with posterior edge of IVth thoracic, and anterior edge of Xth thoracic.

Fig. 5. The IVth thoracic field, with the anterior edge of the VIIth thoracic.

PLATE 44.

Fig. 6. The IIIrd post-thoracic field, the posterior edge of the XIIth thoracic, and the anterior edge of the XIth post-thoracic. The position of the last ribs is marked.

Fig. 7. The Ist and Vth post-thoracic fields, the posterior edge of the Xth thoracic, the anterior edge of the XIth post-thoracic.

Fig. 8. The XIIth thoracic and IVth post-thoracic fields, and the posterior edge of the IXth thoracic. Position of the lowest ribs is marked.

PLATE 45.

Figs. 9 and 10. The VIth post-thoracic field.

Fig. 11. The IIIrd and IXth post-thoracic fields, with the posterior edge of the XIth and XIIth thoracic, and anterior edge of XIIth post-thoracic. Position of lowest ribs is marked.

PLATE 46.

Fig. 12. The Vth post-thoracic field.

Fig. 13. The VIth post-thoracic field.

Fig. 14. The VIIth post-thoracic field, posterior edge of IIIrd, posterior of Xth post-thoracic.

PLATES 47, 48, 49.

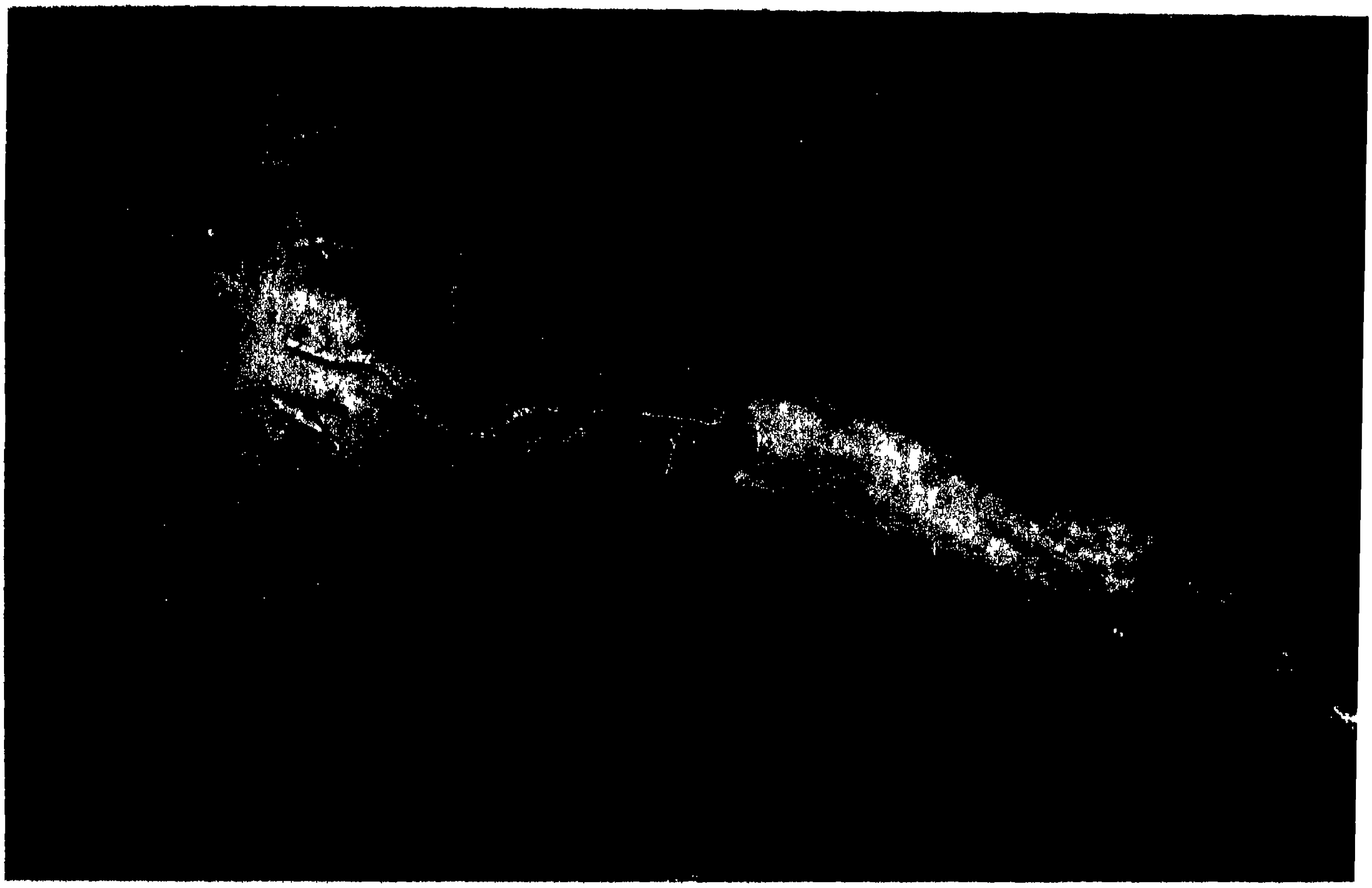
Figs. 15-19 inclusive. Skin-fields from the IVth thoracic backwards, shown on a plaster cast of a young *Macacus rhesus.* The *mid-dorsal line of the limb* is marked in on the left thigh in fig. 19.

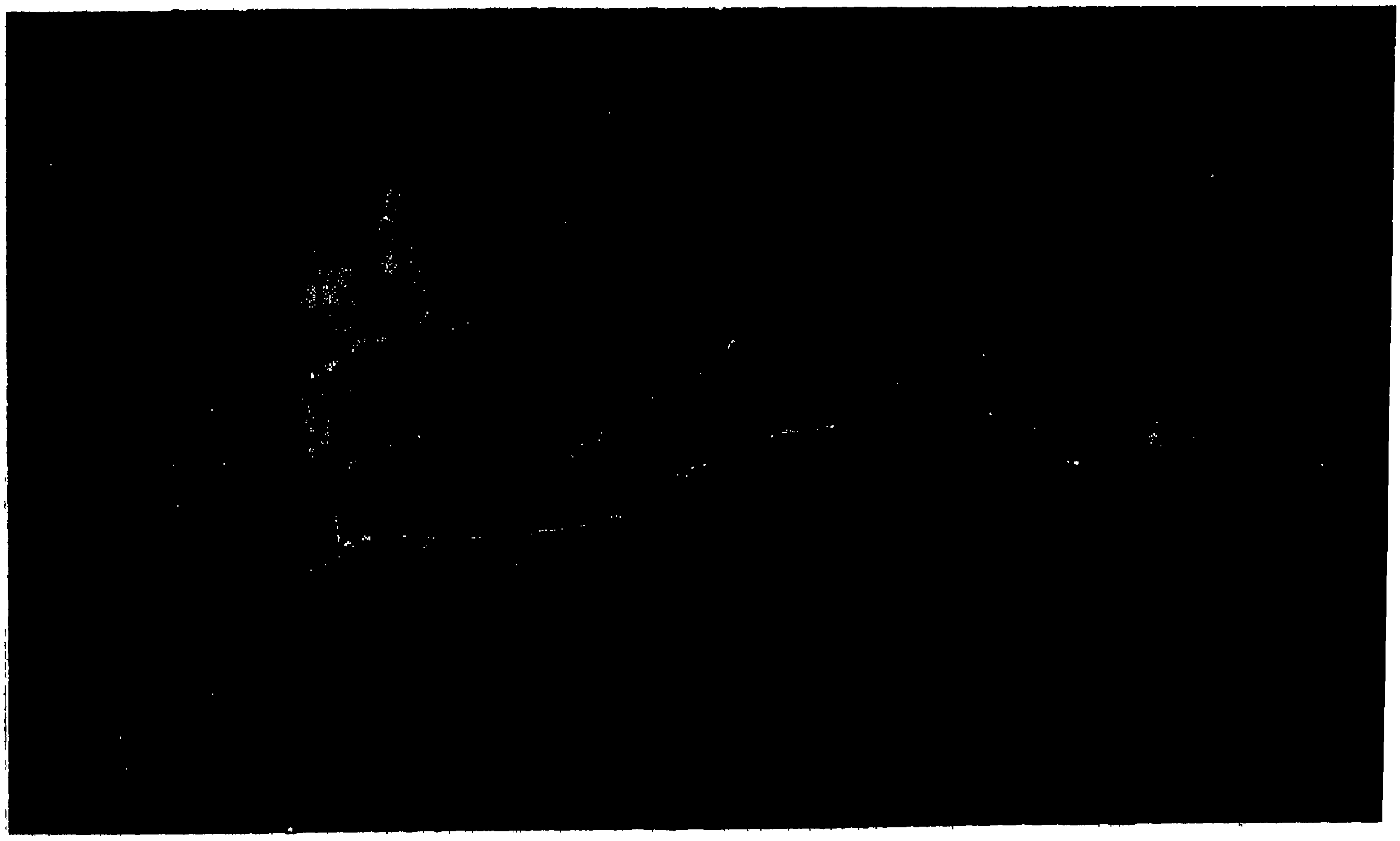
PLATES 49, 50, 51.

Figs. 20–24 inclusive. Similar plaster cast. The anterior borders of the skin-fields are marked on the left half of the cast, the posterior borders on the right half.

PLATE 52.

Diagrams to illustrate the arrangement of the skin-fields, and the terms used in the description.





Sherrington.

Phil. Trans. 1893. B. *Plate* 43.

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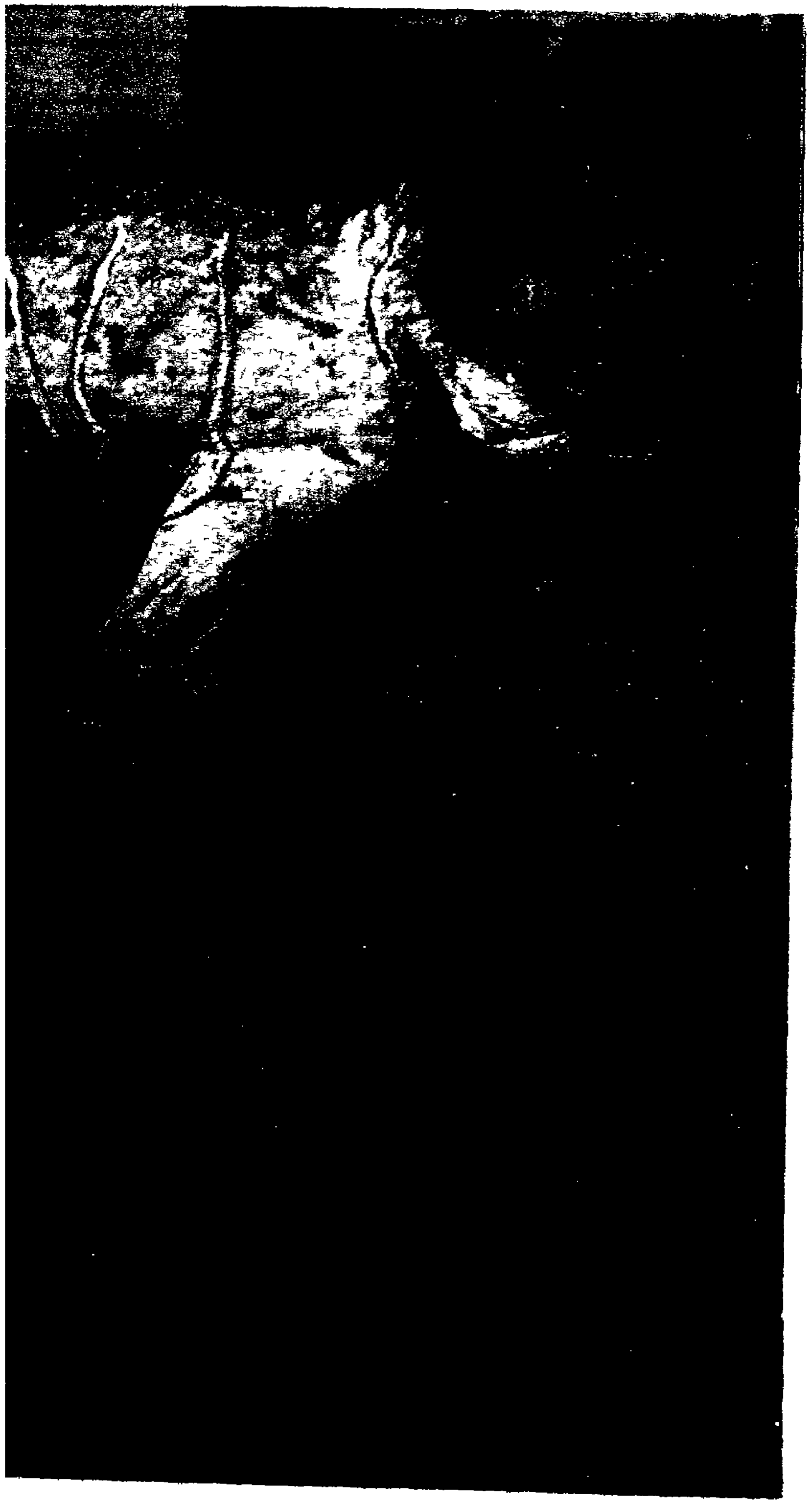

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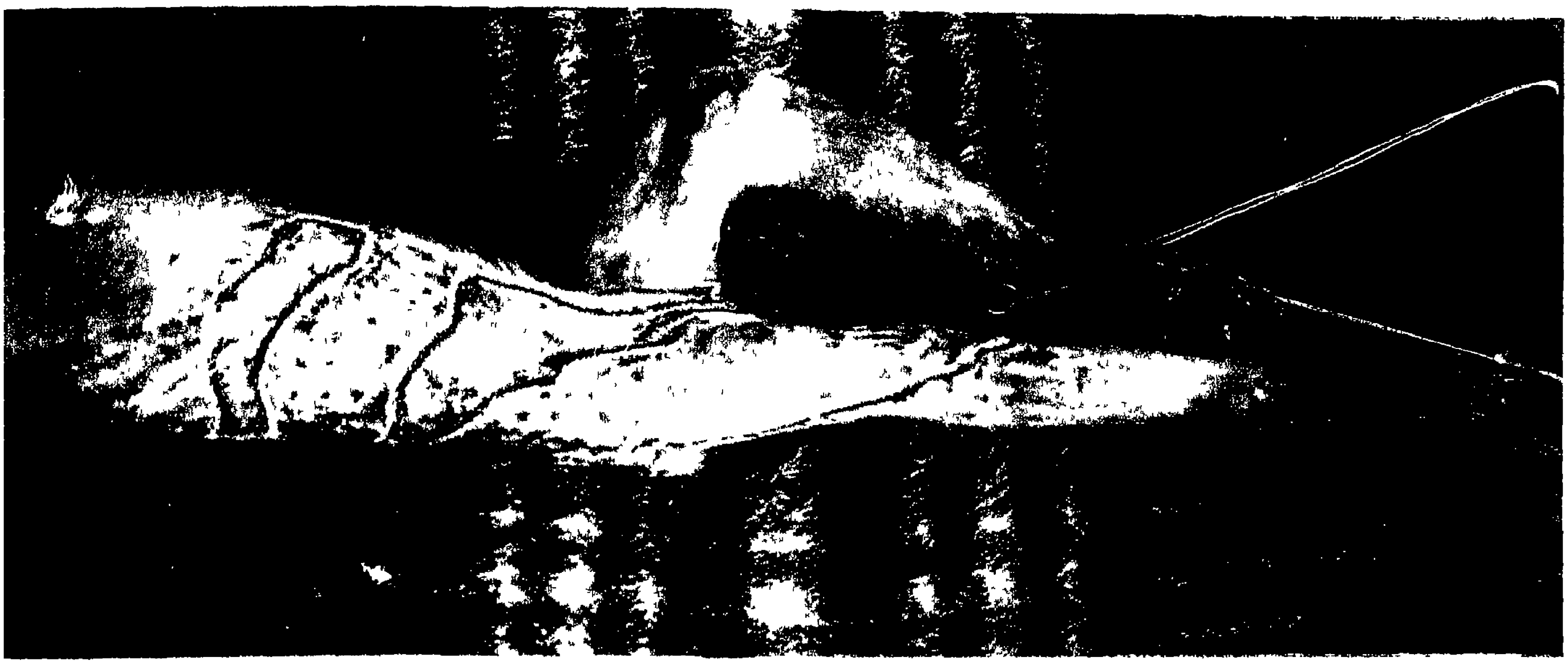

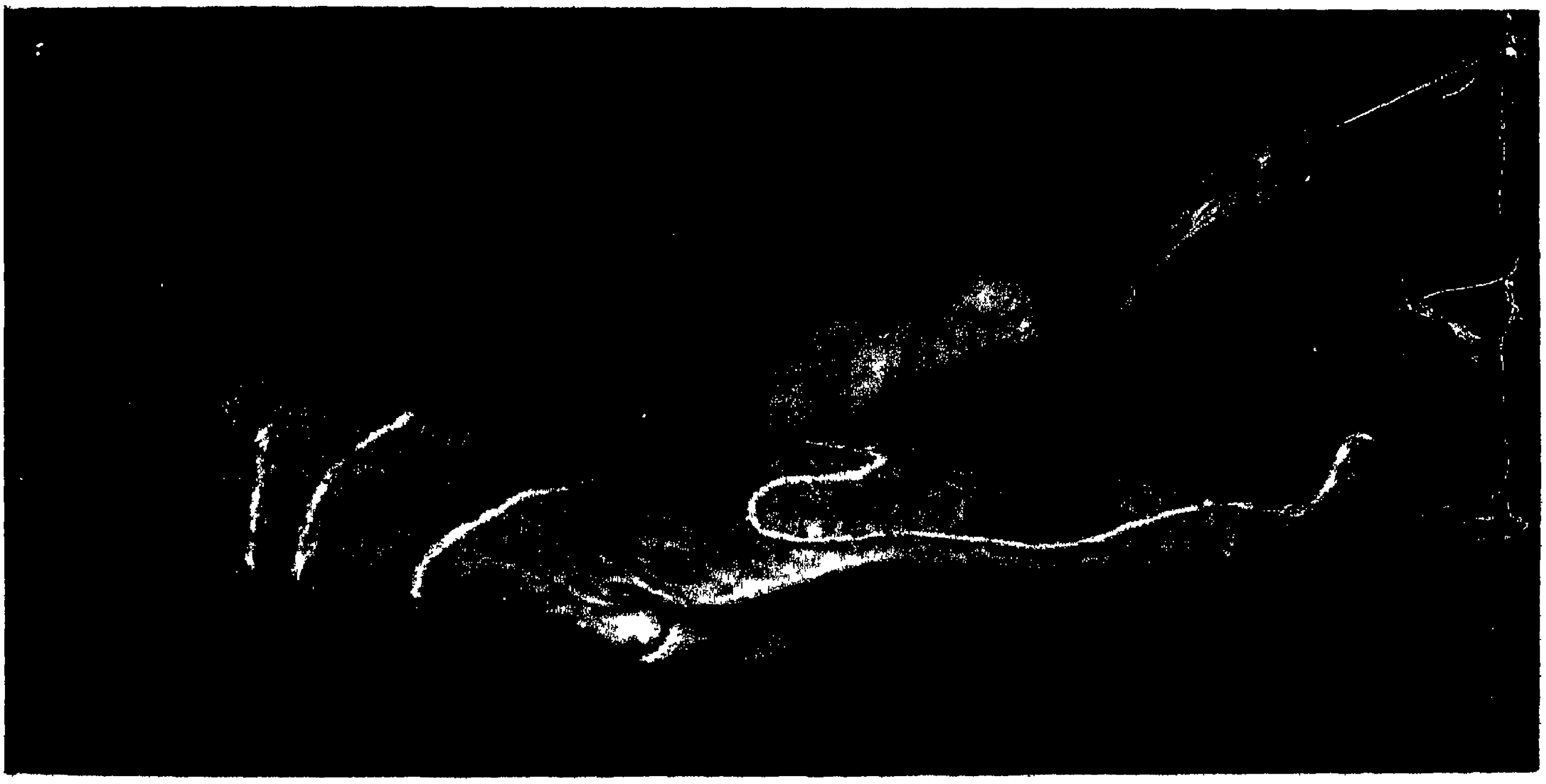

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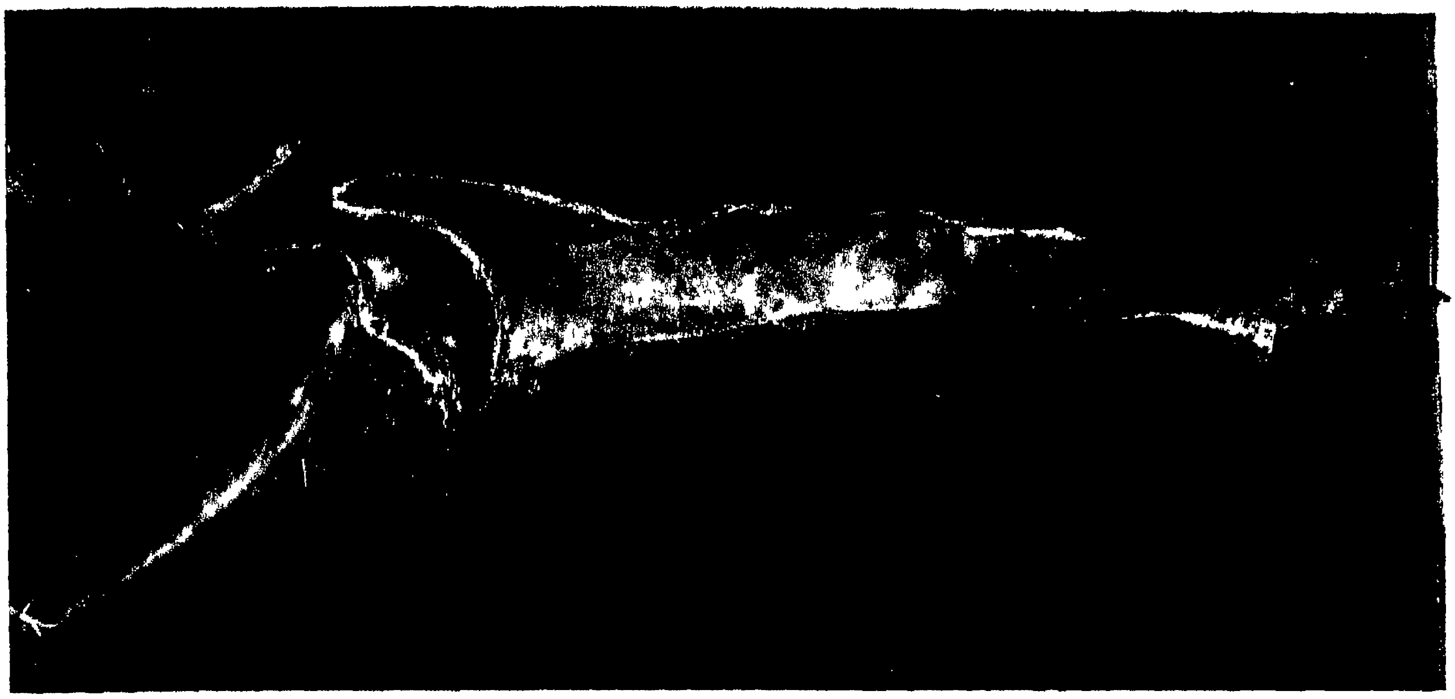

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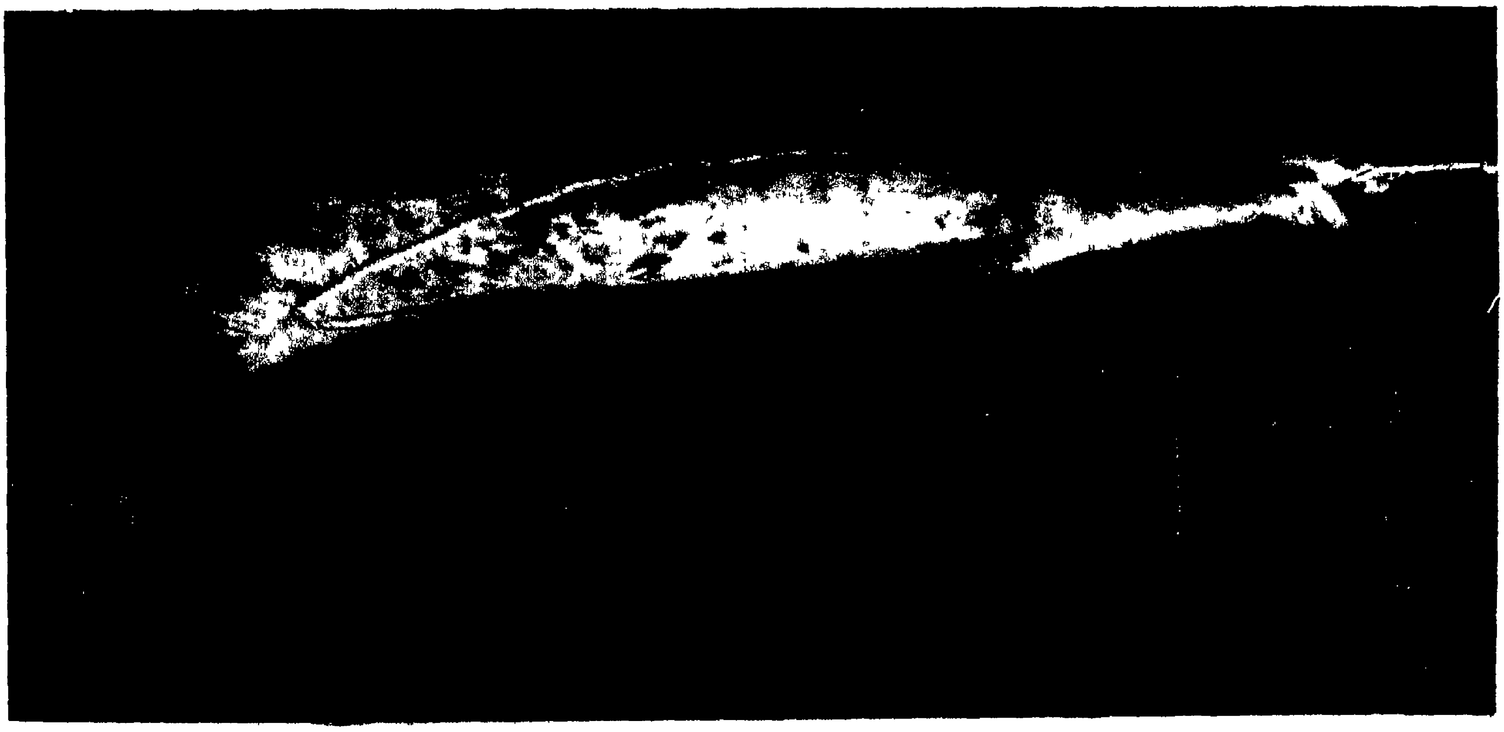

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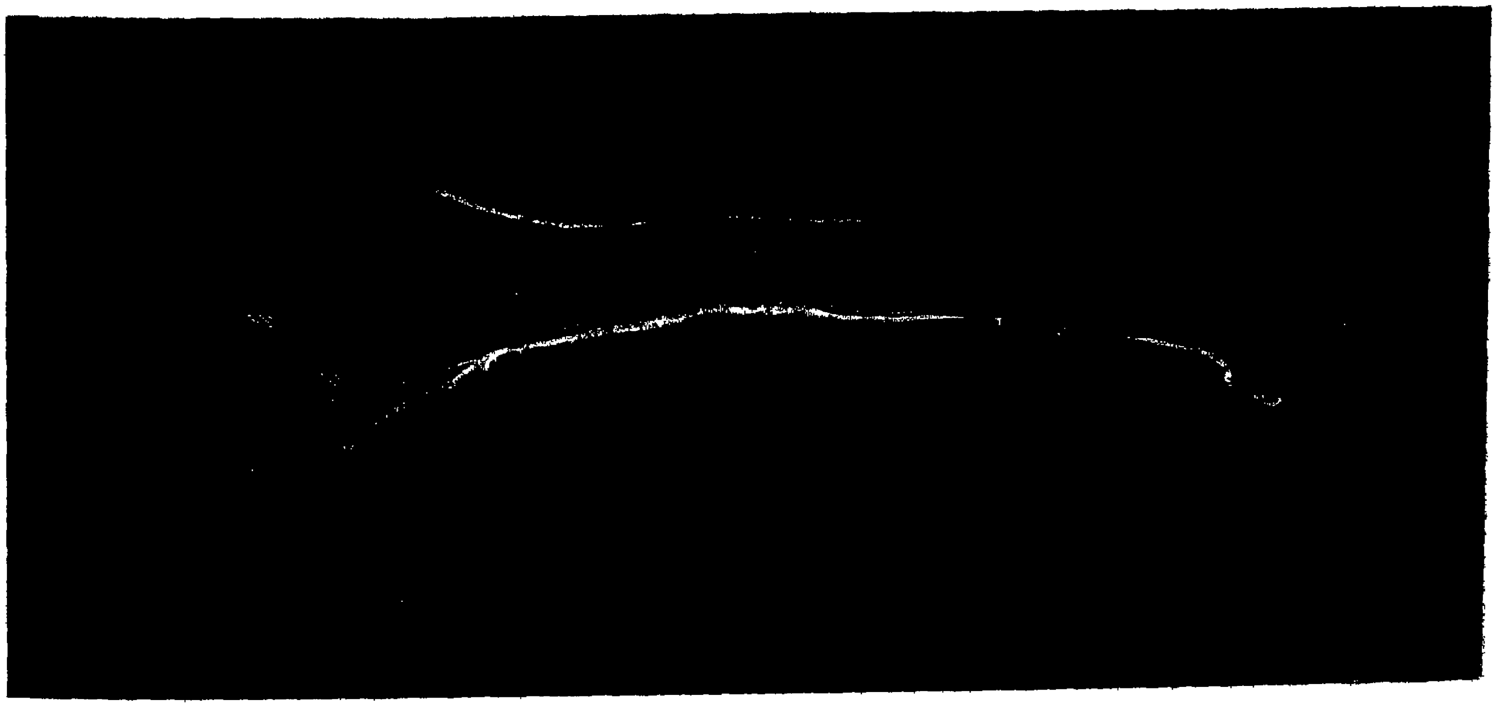

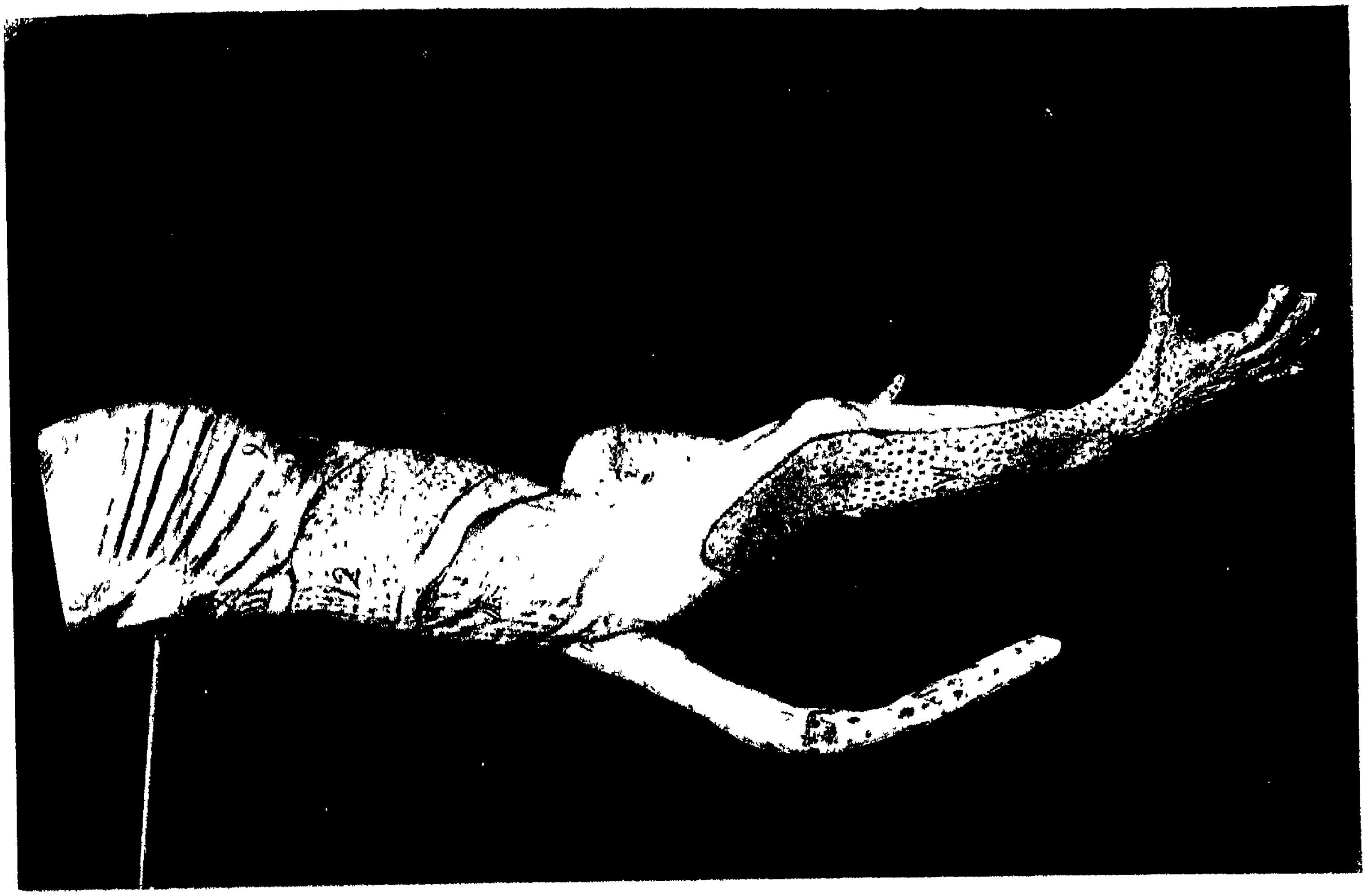

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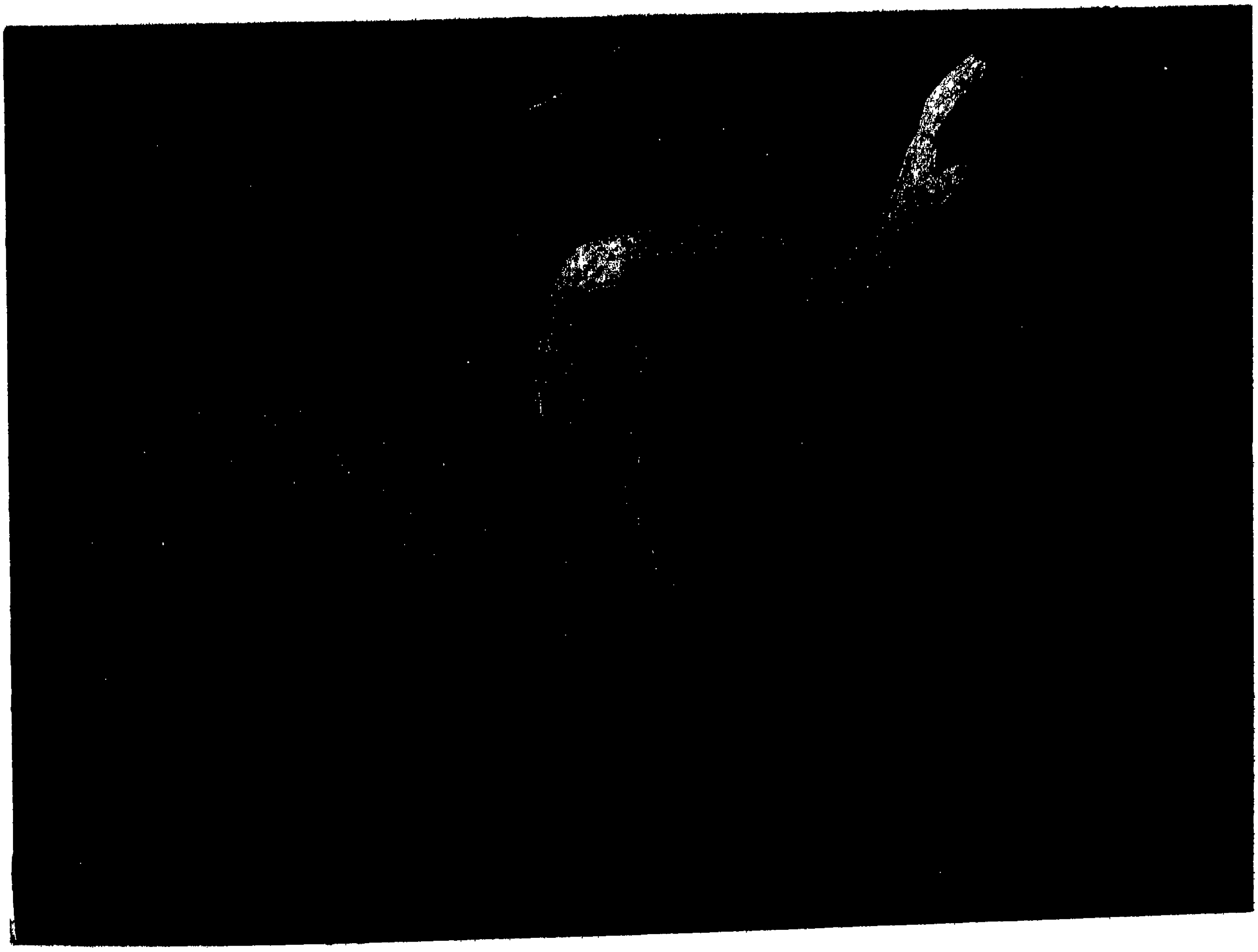

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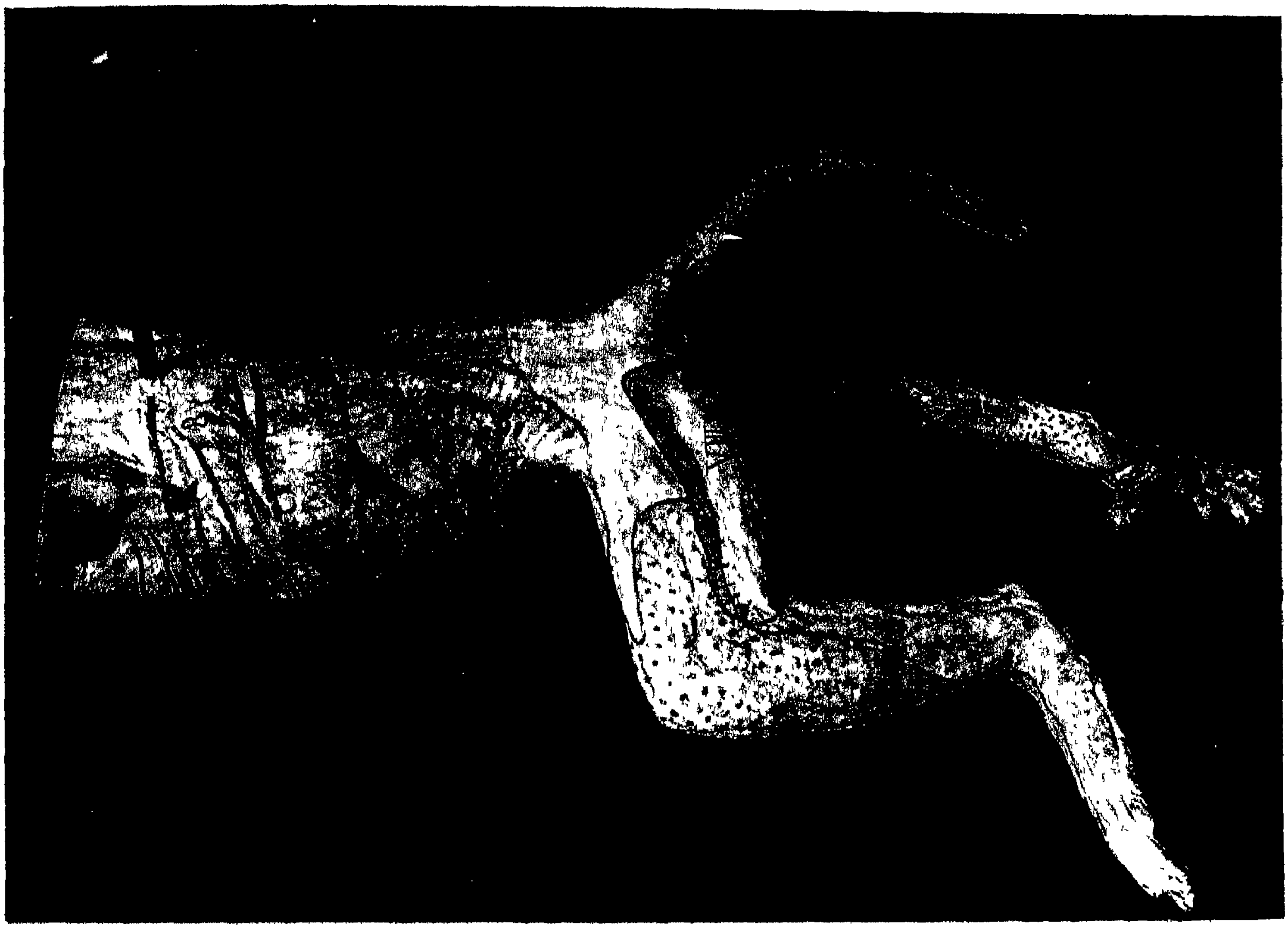

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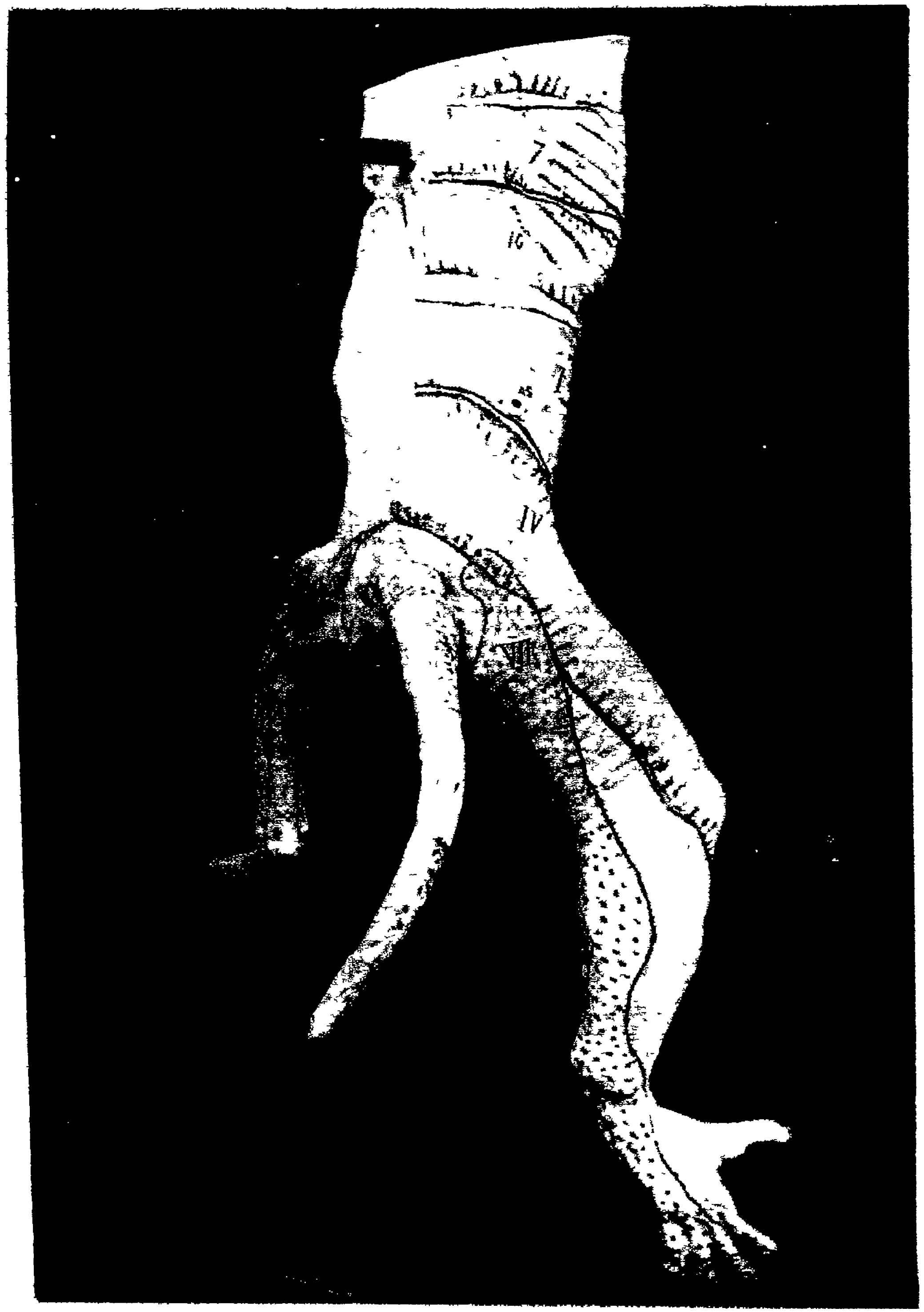

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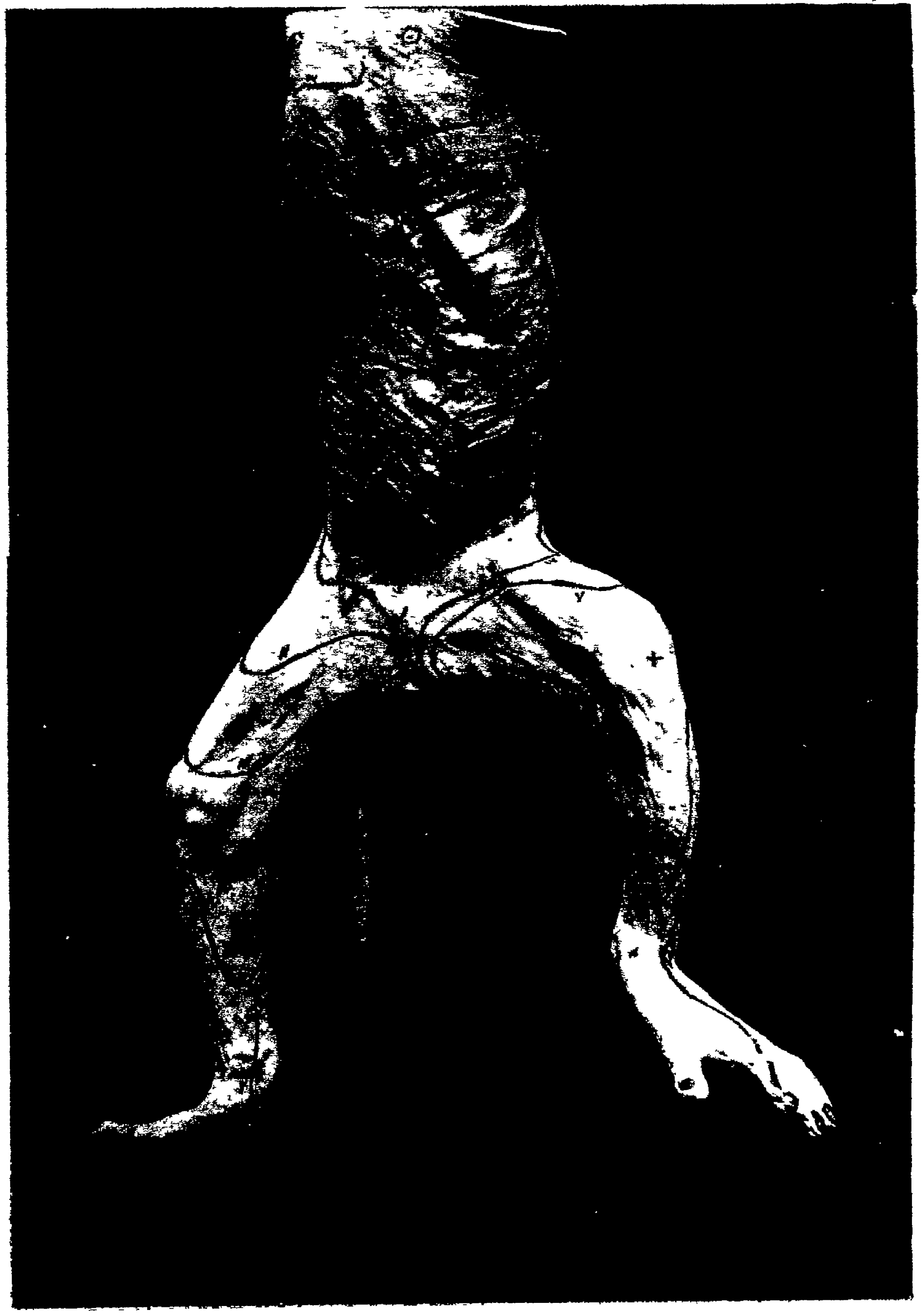

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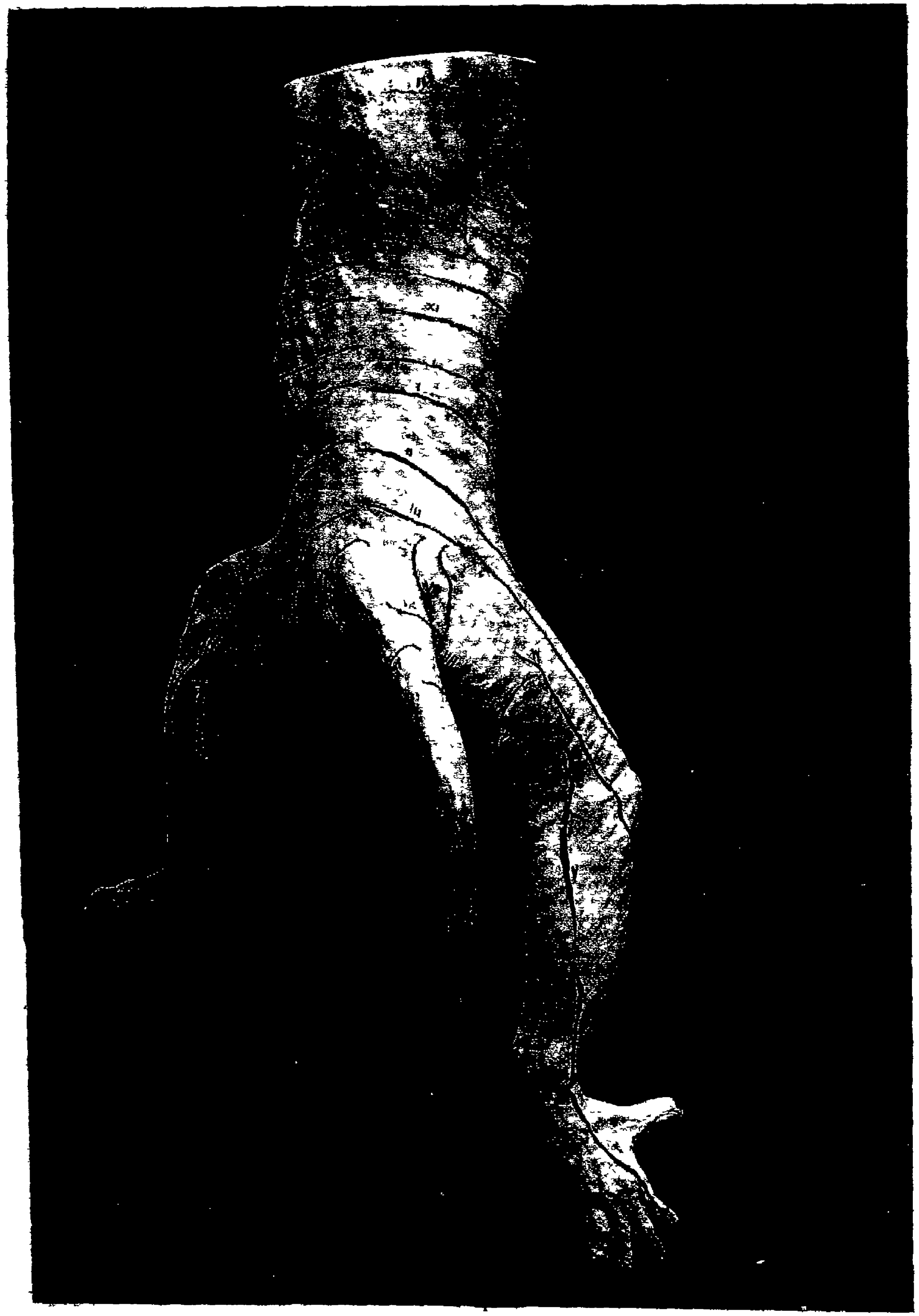

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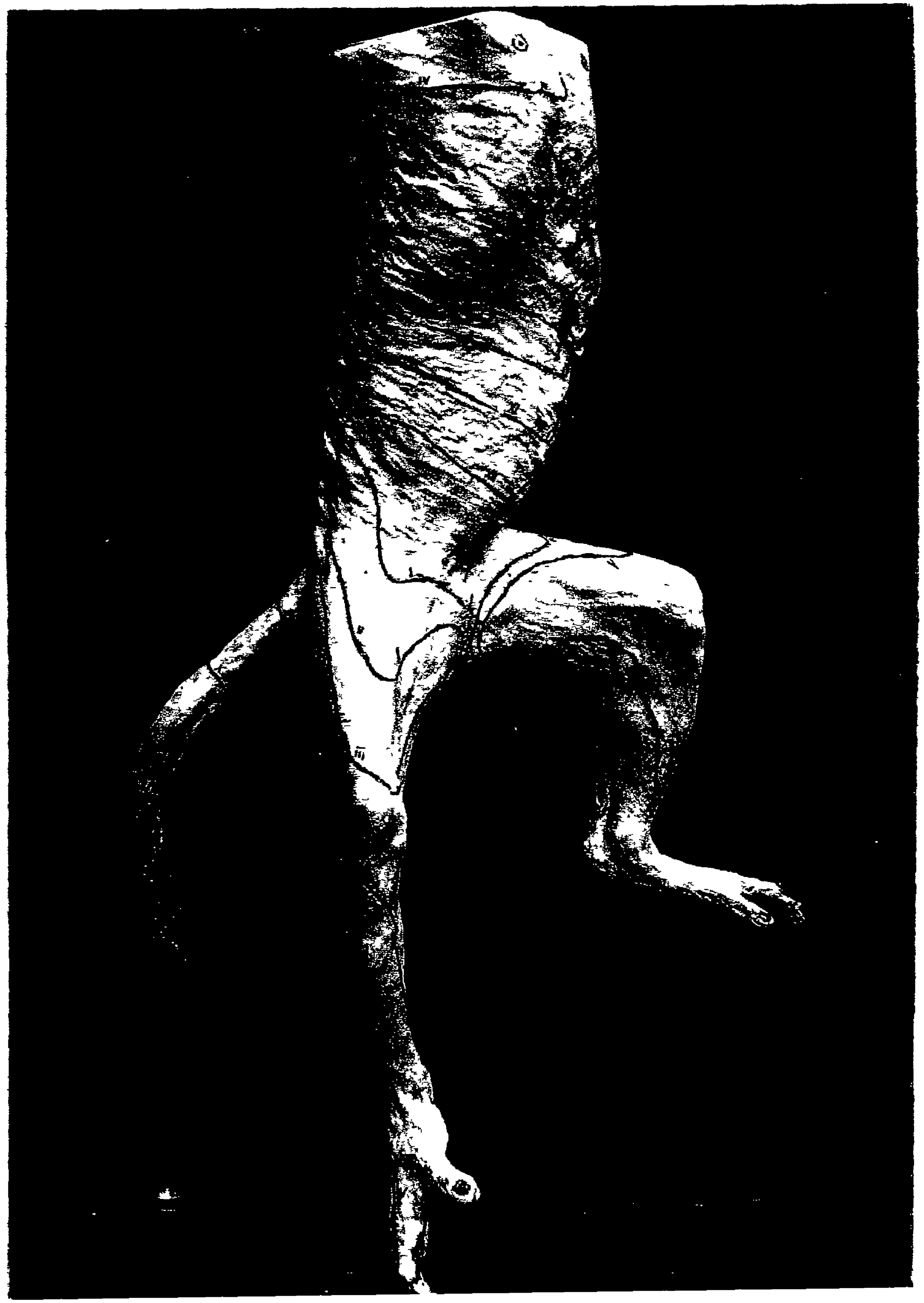

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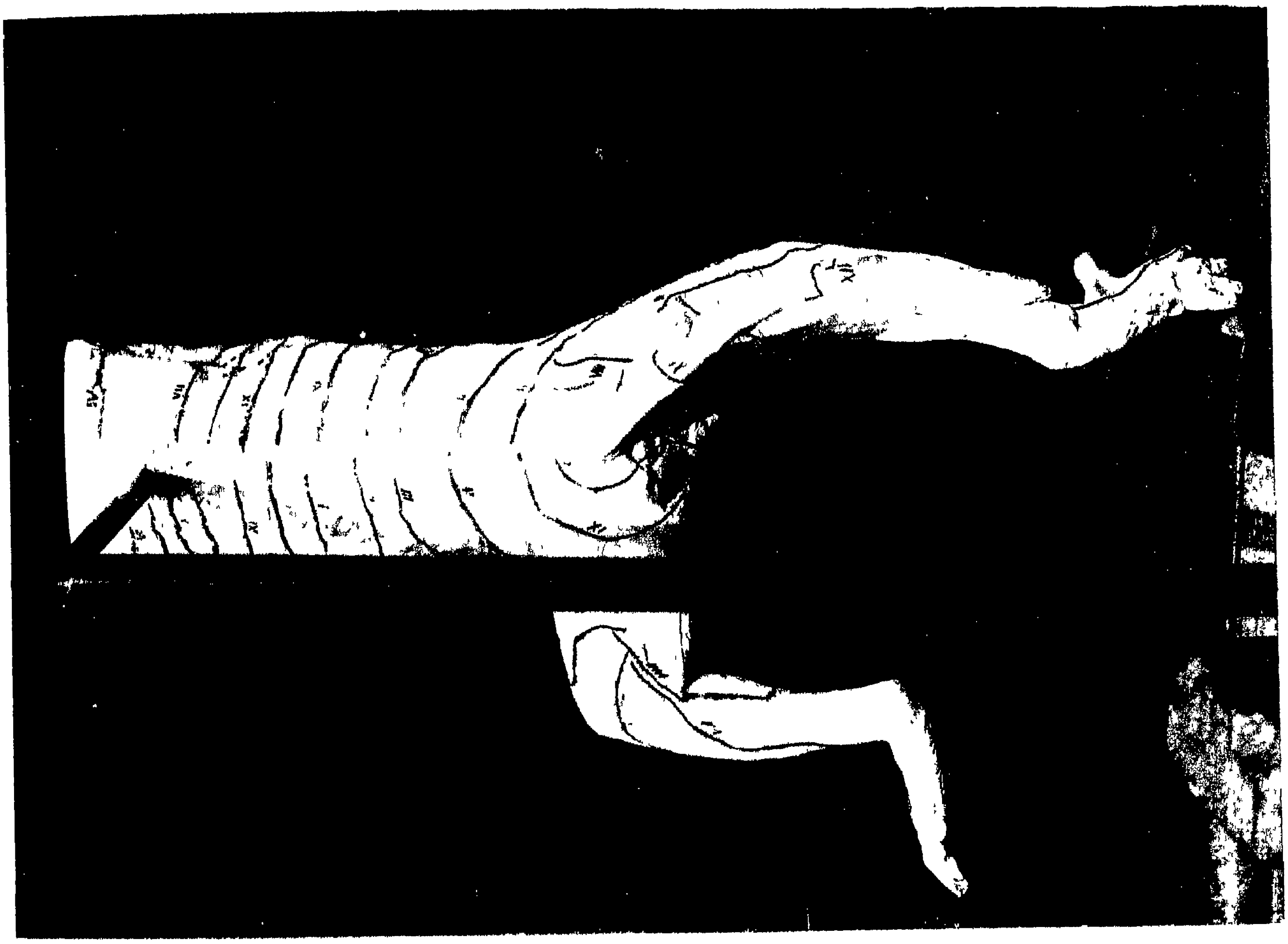

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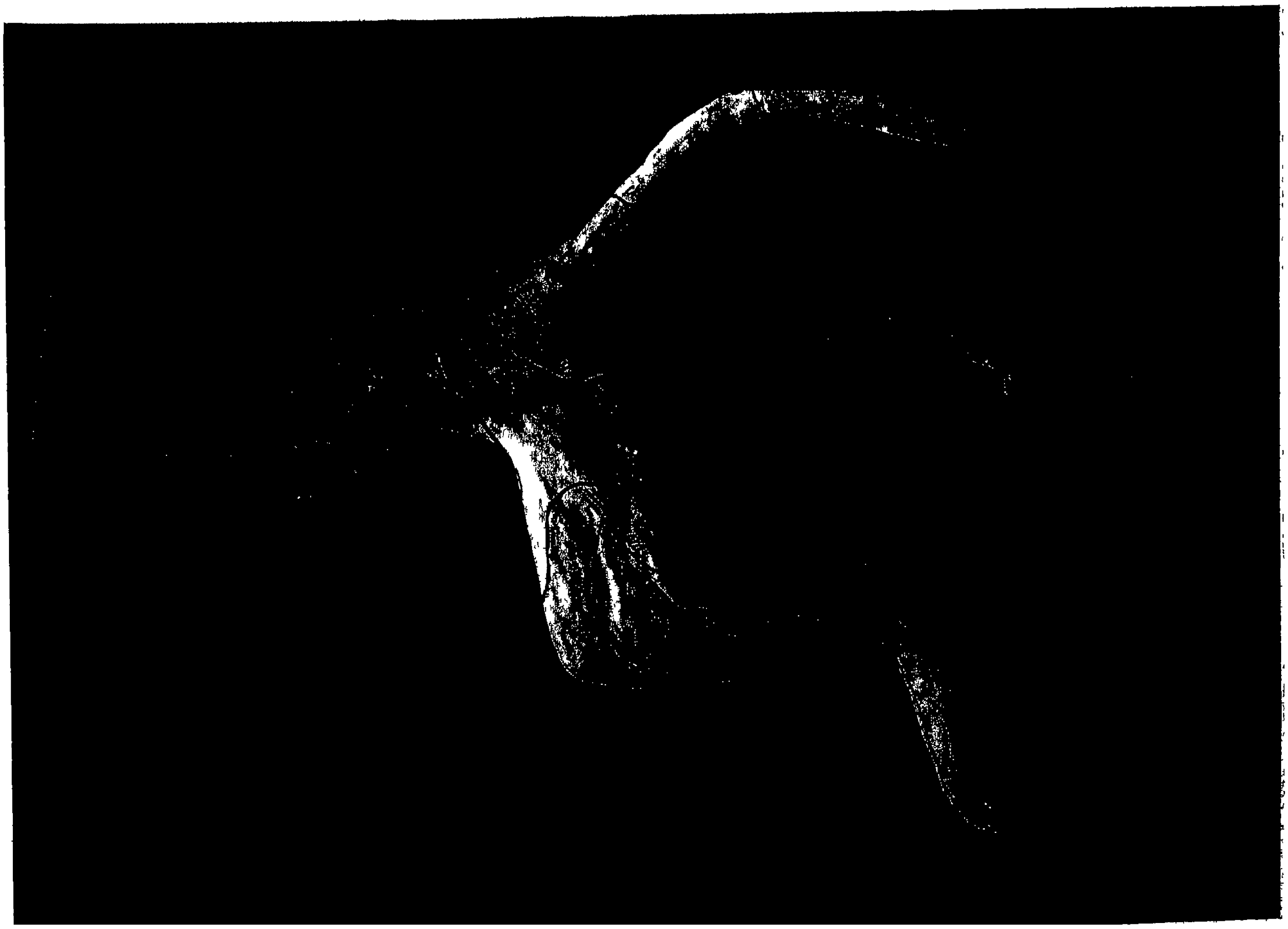

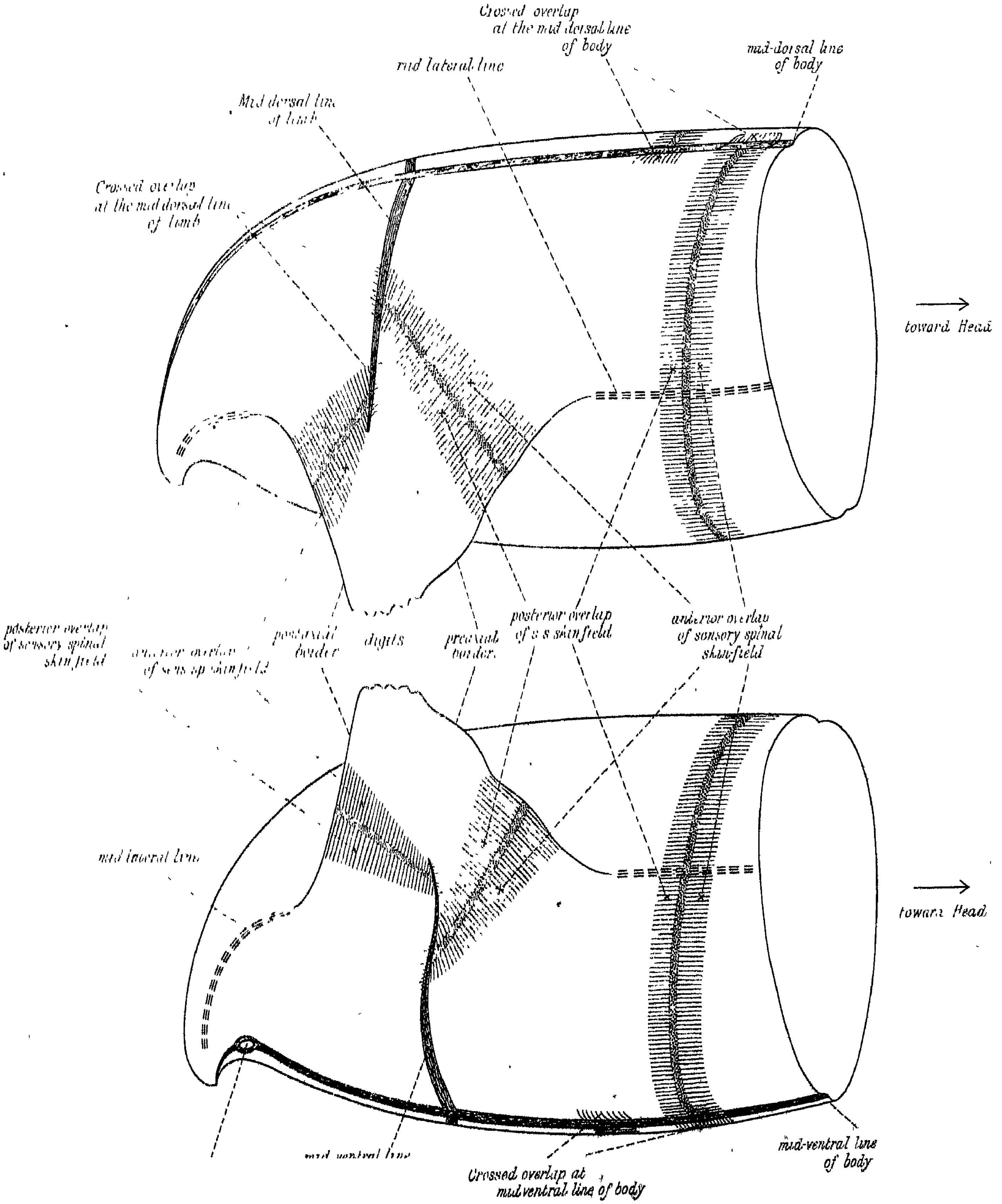
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postaxial border
digits
preaxial border.
posterior overlap of s s skinfield
anterior overlap of sensory spinal skinfield
mid lateral line
toward Head
mid ventral line
Crossed overlap at mid ventral line of body
mid-ventral line of body

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X. *On the Coloration of the Skins of Fishes, especially of Pleuronectidæ.*

By J. T. CUNNINGHAM, *M.A. Oxon., of the Scientific Staff of the Marine Biological Association, and* C. A. MACMUNN, *M.A., M.D.*

Communicated by E. RAY LANKESTER, *M.A., F.R.S.*

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[PLATES 53–55.]

THE investigations which form the subject of this paper were originally commenced with the object of obtaining some reliable definite evidence on the inevitable question, why is the lower side of a Flat Fish white and the upper side coloured? The answer given to the question necessarily involves an opinion on a great many others, and hitherto the terms of the answer have depended rather on the general views held by those who gave it than on a special investigation of the phenomenon. Conversely it was therefore to be expected that a special investigation of the question would have some importance as a test of the truth of conflicting general views and theories. In order to ascertain how far the action of light was capable of producing pigment on the lower sides of Flat Fishes, a series of experiments has been carried out by Mr. CUNNINGHAM, in continuation of one of which an account was published by him in 1891.* But a review of the morphological and chemical relations of the elements and substances of the coloration being necessary for the discussion of these experiments and their results, we have thought it advisable to place this part of the subject first. For Sections III. and IV. of the memoir Mr. CUNNINGHAM is alone responsible, and Section II. is almost entirely the work of Dr. MACMUNN. Both authors have contributed to Section I. The subjects of the various sections are the following :—

- I. Structure and Relations of the Tissue-elements, to which Coloration is due—
    - *a.* Comparative Anatomy,
    - *b.* Histology,
    - *c.* Development.
- II. Chemical and Physical Properties of the Pigments and Reflecting Substance.
- III. The Artificial Production of Pigment on the Lower Sides of Flounders.
- IV. Abnormalities of Coloration in Pleuronectidæ occurring in Nature.

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* 'Zool. Anzeiger,' No. 354.

Mr. CUNNINGHAM's portion of the work was carried on at the Plymouth Laboratory of the Marine Biological Association, Dr. MACMUNN's in his own private laboratory at Wolverhampton.

I.—STRUCTURE AND RELATIONS OF THE MORPHOLOGICAL ELEMENTS OF COLORATION.

(a.) *Comparative Anatomy.*

The various elements in the skins of Fishes which affect the coloration have not hitherto, so far as we have been able to discover, been completely and systematically described or analyzed. Pigment-cells or chromatophores have been frequently investigated, but other elements have received less attention. The most important description of the coloration elements in Fish-skins hitherto published seems to be that of G. POUCHET, in his memoir "On the Changes of Coloration which take place under the Influence of Nerves," published in 1876. POUCHET describes the colour cells in the skin of Pleuronectids and other Fishes under the name of chromoblasts, to distinguish these cells which are characterized by amœboid movements from the pigment cells of Cephalopods, to which he confines the term chromatophores. In this respect we shall not follow him, but shall call the pigment cells of Fishes chromatophores. POUCHET also describes other polygonal cells, which form a layer near the surface of the skin under the convenient name of iridocytes.

He mentions the dense opaque subcutaneous layer to which the silvery brilliance of many Fishes is due, under the name of "l'argenture," and states that it is composed of "lames minces étalées à plat," and states that the same particles distributed confusedly in a tissue act in the manner of transparent substances reduced to a powder and produce a sort of dull silveriness completely opaque. This description applies to the argenteum of Flat Fishes described below, although POUCHET does not mention it in this connection. He recognizes also that the properties of the iridocytes and of the lamellæ of the argenteum are due to the same organic substance, which he says appears to be always of cellular origin, but he does not refer to the fact that this substance is the definite chemical compound guanin, making no mention of the researches of BARRESWIL and VOIT quoted in our next section.

Our own observations have been directed principally to the coloration of the skins of Flat Fishes or Pleuronectidæ, and we shall describe the skins of these in detail, referring to a few other species for the sake of comparison. If a thin superficial slice of the upper side of a Flounder or Plaice is examined under a low power, elements of two kinds are seen, namely chromatophores and iridocytes, forming a beautiful mosaic. The appearance, as seen in the Turbot, has been fairly well figured by POUCHET in the memoir above cited, and the appearance seen in a piece of the skin of the Flounder is represented in Plate 54, fig. 3. The ordinary tissues of the skin of the

Fish, both of the derma and the epidermis, are colourless and translucent in the living condition, and when a superficial slice of the skin is examined in the fresh state these two kinds of elements are extremely conspicuous on account of their colour and opacity, and seem to be set like spangles in a homogeneous translucent material. The chromatophores are distinguished by their colour and irregularity of outline, but the black chromatophores differ in some respects from the yellowish. The chief features of the iridocytes are their regularity of outline, and their great reflecting power; little light passes through them, but when the piece of skin is examined by reflected light they have a very bright spangle-like appearance, although in Flat Fishes they are not very markedly iridescent. Examination of the skin of the Flounder, of fresh specimens and spirit specimens, shows that there is one layer of iridocytes situated outside of the scales, and that the chromatophores are abundant at the same level, scarce in the central layers of the skin. But another deeply pigmented layer is found on the inner surface of the skin, between the skin and the muscles, so that in dissecting off the skin this layer sometimes adheres to it, sometimes remains attached to the muscles. When this layer is examined it is seen to consist of chromatophores exactly similar to those of the superficial layer, and of iridocytes which resemble those of the latter with slight differences. These internal iridocytes are less opaque, and, therefore, have less definite outlines by transmitted light than the others, and they are also much larger. They are also less uniformly distributed than the others, being more closely crowded together in some places than in others; they are very strongly reflective, and more iridescent than the superficial iridocytes.

Examination of the skin of the lower side of the normal Flounder shows that the chromatophores are entirely absent, but the external layer of iridocytes is present and closely similar to that of the upper side of the Fish (Plate 52, figs. 4 and 5). In place of the internal pigmented layer of the upper side there are neither chromatophores nor iridocytes, but a thin perfectly opaque layer of material giving a dead-white reflection. Examined with the microscope this layer presents only a minutely granular structure, and is everywhere uniform and continuous. This layer in other Fishes reflects light in a different manner, so as to produce a silvery appearance, and we shall call it the argenteum. The same distribution of coloration elements is found in the Plaice, *Pleuronectes platessa*, but the argenteum of the lower side is here not so thick and opaque. In the Dab, *P. limanda*, the argenteum on the lower side is still less developed; in specimens about 24 centims. in length it is developed only over the anterior and central regions of the lower side, absent at the peripheral and posterior regions. Moreover, where it is present it is thin, and instead of appearing in a continuous sheet, it is seen to consist of a mosaic of polygonal plates with their edges in contact. The condition of the internal pigmented layer of the skin of the upper side in this species corresponds to that of the argenteum of the lower side, the pigment cells are few and scattered, and the iridocytes still more so. The condition of the argenteum in this species suggests that that layer not only belongs to the same category as the iridocytes, but that it is actually produced by the gradual enlargement and coalescence of separate iridocytes, and we shall show in the next section that the development of the argenteum fully confirms this suggestion. In *Pleuronectes microcephalus* at a length of 28 centims., the condition is much the same as in *limanda*, the internal surface of the upper side contains only scattered chromatophores and iridocytes, while the argenteum of the lower side does not extend over the peripheral region, and is distinctly seen in some preparations to be composed of polygonal plates.

In the Sole (*Solea vulgaris*) the condition is much the same as in *Pleuronectes;* the inner pigmented layer of the upper side is very feebly developed, and accordingly contains but few iridocytes, while the argenteum of the lower side is in large specimens continuous over the whole side, and under the microscope reveals no separate constituent elements. In a large specimen of the Sole which had been for some time in spirit, we found that the skin of the lower side could be stripped off entire, without disturbing the argenteum, which remained attached to the flesh.

In *Arnoglossus megastoma* the colour of the upper side is a light brown, while the lower white side is not an opaque chalk-white, as in the Flounder or Turbot, but translucent. On examination it is found that the outer layer of skin of the upper side outside the scales contains black chromatophores, not very closely crowded, and somewhat thin and translucent when expanded; also orange-yellow pigment in chromatophores, and rounded iridocytes. On the inner surface of the skin on this side there are also streaks and spots of colour composed of black and yellow chromatophores, and scattered iridocytes more brilliantly iridescent than those of the outer layer. On the lower side the outer layer outside the scales contains thin separate iridocytes closely arranged to form a mosaic; these are rather opaque to transmitted light, but by reflected light appear dull white, not silvery or iridescent. On the inner surface of the skin of the lower side we have been unable to detect a trace of argenteum or of iridocytes. The skin of this Fish is remarkable for the large number of prismatic crystals which it contains. They are transparent and have no effect on the coloration; they are situated at various depths in the skin and are not soluble in fresh water.

Before considering more minutely the chromatic elements as they occur in Flat Fishes, it will be convenient to ascertain how far those found in the skins of other Fishes agree with them in general character and distribution. The Gadidæ are supposed to be the nearest allies of the Pleuronectidæ, and we may therefore begin by examining the Whiting, *Gadus merlangus.* In this species the sides have a beautiful iridescence and silvery lustre, the belly is dead white, with scarcely any metallic brilliancy, the back is a dark bluish-grey. Examination of the entire Fish, and with the unaided eye, shows that the chromatophores are densest over the back, [illegible] crowded over the sides, absent on the belly. If the portion containing [illegible] sliced off with a razor and examined under the microscope, it is found that the irisdescent silvery surface is due entirely to a layer of iridocytes on the external sides of the scales. But these iridocytes are very different in form and arrangement from those of the extralepidar portion of *Pleuronectes.* Instead of being polygonal plates distributed at a certain distance from one another, they are short narrow rods or spindles, placed close together side by side, so as to form an uninterrupted sheet. Lying upon them are black stellate chromatophores of the usual kind, and beautiful deep yellow chromatophores, which also exhibit a radiate dendritic form, their branches extending far from the centres. Here, then, we have structures closely corresponding to those found in *Pleuronectes*, only the shape of the iridocytes is very different, and their metallic lustre and iridescence vastly greater. When the superficial layer of the belly is examined these iridescent iridocytes are not seen, their place is taken by a thin layer of granules arranged in parallel wavy lines having little opacity and no iridescence. On the other hand, when the corresponding layer of the back is examined, closely crowded black chromatophores are seen intermingled with yellow, but here also the iridocytes are absent, represented if at all only by minute granules discerned with difficulty between the chromatophores.

After the superficial layer containing the scales has been removed with the razor, the part of the skin left behind is still opaque and silvery, and contains scattered chromatophores. If this portion is sliced off and examined with the microscope, the silvery reflection and opacity is easily seen to be due to a thick layer on the inner side of the skin, next to the muscles. This layer is so thick and opaque that it is difficult at first to make out any structure in it with the microscope, but where it has been crushed a little or broken, it is seen to consist of rods like the iridocytes, but considerably smaller: where the layer is thus made thinner some iridescence appears, but in the normal state there is no iridescence, only silvery reflection. The chromatophores are similar to those of the outer layer. On the belly the argenteum is well developed and continuous, but there are no chromatophores on the inner surface of the skin. On the back the inner chromatophores are well developed, but there is not a trace of argenteum or of iridocytes on the inner face of the skin in the dorsal region.

In *Trigla lyra* examination of the entire Fish shows that the sides are slightly though not very brilliantly silvery, while the belly is white and the back red. When the outer layer containing the scales from the lateral region is examined under the microscope, the silvery layer is seen to consist of strands of opaque tissue, arranged not in separate iridocytes, but in a dense net-work ; the strands themselves consist of rod-shaped minute granules, very much smaller than the rods in the Whiting above described. Over the silvery layer are brick-red chromatophores, for the most part in the form of small round spots, and showing little tendency to branch. On the back the silvery layer is evanescent, represented only by a thin layer of rounded granules, which is by no means opaque to transmitted light, and by reflected light gives only a faint silvery shimmer reminding one of pearl-dust. Besides the red there are large dendritic black chromatophores and patches of diffused light yellow pigment, which contrast strongly with the other two pigments. The skin of the Gurnard is very thick, and, in the dead Fish, more opaque than usual; yet, on the inner side in the lateral region, we find a dense opaque argenteum with a somewhat silvery lustre, which contrasts strongly with the leathery skin. On the back the argenteum is wanting; on the inner side of the skin are found black dendritic chromatophores and patches of diffused yellow pigment, and here and there a thin iridocyte or patch of argenteous matter, of no constant or regular shape, and having a greenish yellow reflection.

On the belly the chromatophores disappear, and the layer of opaque tissue becomes considerably thicker, losing its property of silvery reflection and becoming chalk-white.

In *Trigla cuculus* the coloration elements are closely similar, but the silveriness of the lateral regions is much less marked than in *T. lyra*. The inner argenteum is well developed on the lateral region and the belly, and somewhat more developed on the back than in *T. lyra*. The outer pigmented layer of the pectoral fin in *T. cucul u* is represented in Plate 55, fig. 5, as it appears in the fresh state under the microscope. In this species black chromatophores are scarce in the lateral region, and none came within the part of the field represented. The minute iridocytes have a slightly bluish tint when examined by transmitted light. These minute iridocytes in *T. cuculus* correspond to the granules which compose the strands of tissue in the same region of *T. lyra*.

In *T. gurnardus* the same general distribution of elements is found. The cause of the difference of colour between this and most other species of Gurnard, the former being grey and the latter red, is simply the greater abundance of black chromatophores in the former, and of red in the latter. The sides are slightly silvery, and the elements producing the reflection are somewhat larger than in *cuculus*, while they become smaller on the back. The appearance of the dorsal region above the lateral line in *Trigla hirundo* is shown in Plate 55, fig. 6.

The Gurnards and *Cottus* are placed in the same family, Cottidæ, by most systematists, but they do not resemble one another in their coloration. In the common *Cottus bubalis* there is no argenteum, except on the under surface of the head, and thence backwards over the ventral side in the abdominal region. In the fresh state, if the skin is dissected off in this region it separates easily and the argenteum is left behind, forming a thin silvery film over the muscles. Under the microscope this argenteum is seen to consist of thin irregularly-shaped plates irregularly distributed, in some places contiguous with one another on all sides, in others leaving considerable intervals unoccupied. Here and there a little diffused yellow pigment is seen among the plates of reflecting substance. In *Cottus* there are no scales, except in the lateral line, but, nevertheless, the coloration elements are situated in the superficial layer of the skin. They consist of large black stellate chromatophores, much smaller red chromatophores, which in some parts of the skin are separate and distinct, while in others they form an inextricable network, of a diffused yellow pigment, and of a network of reflecting substance, which is closely associated in most parts with the large black chromatophores. It goes without saying that the different colours of different parts, patches, or spots of the skin of the *Cottus* are produced by the preponderance or exclusive presence of one or other of these elements. The opaque white spots are due to a thick mass of the reflecting substance, the black to an excess of black chromatophores, red and yellow parts to excess of red or yellow pigment. The general colour of the specimens found on the shore or in shallow water is dull grey or brown, but specimens are not unfrequently obtained from deeper water which are bright red or crimson nearly all over the dorsal region. The difference in the latter case is entirely due to the greater abundance of the red pigment which forms a network of lines, and the diminution in the number of black chromatophores. These differences are shown in figs. 1 and 2, Plate 55.

In the fishes of different families thus far examined, we find that the coloration elements are chiefly deposited in two layers in the skin, outside the scales, and on the inner surface of the skin; that where the chromatophores are most developed, namely, in the dorsal region of the body, the reflecting tissue is, to a greater or less degree, evanescent, and *vice versâ;* and, lastly, that where iridescence is developed it is due to the outer reflecting layer, while the inner layer presents either a chalk-white opaque surface or an evenly bright silvery surface. In examining representatives of a few other families, we shall not find these generalizations contradicted except in trifling details.

The distribution of the elements in the Mackerel, for instance, is somewhat different from that in the Fishes previously mentioned. The scales are very deciduous in the Mackerel, and of course when the scales separate, the epidermis and the part of the cutis which covers the scales externally are lost too. A Mackerel obtained as fresh as possible on the fish-quay has lost all its scales except a few loose ones at the base of the fins, and those of the lateral line, which remain firmly attached in the skin. But the brilliancy of coloration of the skin is not apparently diminished, the sides and the belly gleam with the most vivid iridescence, changing from silver to yellow or red gold according to the angle at which the light is reflected to the eye, and the back is marked with the familiar wavy bands of black and green alternately. It is evident, therefore, that the colours of the Mackerel are not principally situated in the outer layer of the skin which contains the scales. Now, the skin of the Mackerel in this condition can be easily separated in large sheets from the body, and it comes off as a transparent tough membrane with very little colour, leaving the colour and iridescence of the Fish more brilliant than ever. Thus the chromatophores on the inner surface of the skin and the argenteum in the same position produce the coloration of the Mackerel, with scarcely any appreciable aid from the outer layer. If we examine the translucent skin stripped off, however, we find that it contains a few chromatophores.

The sockets of the scales are left on the surface of the skin in the dorsal region, and for some distance below the lateral line, as somewhat rhomboidal areas bounded by thickened bands in which black and yellow chromatophores are conspicuous. These bands represent the outer layer of the skin which has been broken through by a large aperture wherever a scale has fallen out. In the central parts of the scale-scars, that is, in the skin beneath the scale, no chromatophores are to be seen. Along with the chromatophores, and especially around the black ones, a little granular reflecting tissue is to be seen, but it is insignificant in quantity. On the scales of the lateral line which remain *in situ* the black and yellow chromatophores are more abundant and uniformly distributed. Also when the few loose scales still adhering to the skin are examined their outer sides are found to contain the same black and yellow chromatophores. It is a curious fact that, although these yellow chromatophores by transmitted light are always yellow under ZEISS, A., or a higher power, and appear dim yellow when the light is cut off from below, yet there is one condition under which they appear distinctly green, namely, when seen with ABBE's substage condenser and his centre-spot diaphragm. The reason of this is probably that they are then seen against a black back-ground.

When the internal layer of the skin in the dorsal-coloured region is examined, black and yellow chromatophores are seen closely crowded together. The black bands are caused by the greater abundance of the black chromatophores and diminution of the number of yellow. In the green bands the two kinds of chromatophores are equally abundant, and the blending of the two colours produces the green. Over the dorsal and lateral regions of the Fish, where the black and green coloration extends, the reflecting layer is also present, the chromatophores lining the inner surface of the layer. But here the argenteum is so thin that the colour of the chromatophores appears through it, and its effect is to give a silvery reflection and some iridescence to the skin. Towards the belly the chromatophores disappear, and the argenteum becomes thicker and much more opaque. The iridescence as well as the silvery glitter are thus, in the Mackerel, produced by the surface of the argenteum itself.

It is interesting to compare the coloration elements in different Pipe Fishes (Syngnathidæ), and trace the ultimate causes of their differences in colour. Thus, the commonest species, *Syngnathus acus*, is of a general brown colour, marked with darker and lighter transverse bands alternately. On the belly the brown colour is absent, the skin is very light, with a golden yellow tinge becoming deeper toward the centre. The ventral surface of the tail is almost colourless, except towards the extremity, where it becomes brown, like the dorsal skin. On examination it is found that there are scarcely any coloration elements on the inner surface of the skin in this species, only a few scattered chromatophores. On the outer side of the bony scutes [illegible] the elements which give the Fish its colour. On the sides of the body there are, [illegible] layers of the skin, black chromatophores of the usual kind, in the interspaces [illegible] a variable quantity of orange pigment, not in definite chromatophores, but irregularly deposited in granules and globules; this pigment becomes more red or lighter yellow, according to the thickness of the deposit. The black and orange pigment together produce the brown colour, when blended, as seen by the unaided eye. Beneath the chromatophores there is a loose reticulation, or felting, of anastomosing strands composed of multitudes of minute short rods. This layer has a feeble reflecting power, and is the cause of the greyish opaque white of the skin, which is seen where the chromatophores are scarce. On the dorsal side of the body this reflecting tissue is absent, while the black chromatophores are closely crowded together. On the ventral side the reflecting tissue is well developed, and there is an abundance of the orange pigment, but the black chromatophores are almost entirely absent.

The difference in colour between *Siphonostoma typhle*, a green species of Pipe Fish which lives among the blades of the sea-grass *Zostera*, and affords a typical instance of protective resemblance, and the brown *Syngnathus acus* is, as far as we have been able to discover, entirely due to the difference between the yellowish pigments in the two Fishes. As we have seen, this pigment in *Syngnathus* is an orange yellow which, when blended with black, makes a brown, but in *Siphonostoma* the yellowish pigment is a lemon yellow with no approach to red, and this yellow, blended with black, produces an olive green (figs. 3 and 4, Plate 55). The green of the back of the Mackerel is similarly produced by the blending of black and lemon yellow.

Specimens of *Siphonostoma typhle* are usually green, but we have seen one, a male, which appeared brown. In a green female the ventral side of the tail is as green as the dorsal side, but in front of the anus the colour instead of being dark olive green, is light greenish gold. There is an outer pigmented layer outside the scutes, and, as usual, a pigmented layer on the inner surface of the skin beneath the scutes. The outer layer when shaved off with the razor and placed under a microscope, is found to contain numerous black chromatophores and a large quantity of lemon yellow pigment, filling entirely the spaces between them; the combination of these gives the green colour, and the yellow pigment itself appears green when examined by the light of the centre-spot diaphragm. On the ventral abdominal surface both black and yellow pigments are extremely scarce. No definite iridocytes or reflecting elements are discernible in this outer layer of the skin. On the inner surface of the skin there are disconnected patches of black pigment in chromatophores, with diffuse yellow pigment similar to that of the outer layer, and associated with the black chromatophores some reflecting tissue which is small in quantity, but is very remarkably iridescent, appearing for the most part a deep metallic blue by reflected light. This blue doubtless aids a little in producing the green coloration of the skin, but not much, because there is so little of it, and it occurs only in separate small patches. This inner pigmentation is most developed on the back and sides, where the pigment in the outer layer is also most abundant. There is scarcely any of it on the ventral abdominal skin, the golden colour of which is entirely due to the peritoneum, appearing through the body wall, which is there thin. The peritoneum consists of a beautifully iridescent argenteum on the free surface turned towards the body cavity, and beneath this, towards the skin, an abundance of large black chromatophores and golden yellow pigment; the yellow pigment is most external, so that when the outer side of the peritoneum is exposed, it presents a continuous yellow surface, while the inner surface is a combination of iridescent silver and black. At the dorsal side of the body cavity, when that cavity is laid open, the peritoneum is black without silvery glitter, that is to say, the black pigment is most abundant dorsally.

The Clupeidæ resemble the Mackerel in their pelagic mode of life, and in the brilliant silvery glitter and iridescence of the skin, but minute examination shows that the elements on which the coloration depends are not distributed in exactly the same way. The chief difference is the presence of a thin layer of rod-shaped iridocytes on the inner side of each scale. This layer exhibits the most brilliant iridescence; it is not very opaque because it is so thin, but when light reflected obliquely from it enters the eye, it reminds one of the iris which changes on the burnished dove. The properties are very permanent, and remain unaltered for any length of time in a scale mounted on a slide in glycerine jelly, or FARRANT'S solution. There are also chromatophores, black and yellow, as in the Mackerel, on the outer side of the scales in the coloured regions of the body, namely, the back and sides. On the inner side of the skin, as in the Mackerel, there is a thick argenteum, with a bright silvery surface on the belly and sides; it becomes evanescent towards the back, and there chromatophores, which are absent on the belly, and scarce on the sides in this part of the skin, become abundant.

Atherina is a genus widely separated from the Clupeidæ, belonging to the *Physoclisti*, and approaching somewhat the Grey Mullet in general structure. In its coloration and adornment, however, it presents a peculiar feature, not seen in any of the species yet considered, and only matched in the genus *Osmerus* among the Salmonidæ. *Atherina presbyter* is common on the South Coast of England, where it replaces the true Smelt (*Osmerus*), and is usually known under the name of the latter. In the region of the lateral line of this little Fish there is a very distinctly defined and very brilliant silvery band, about 3 millims. wide, and running the whole length of the body. Dorsal to this band the skin has no silvery brilliance, but is pigmented, the pigment marking out very distinctly the outlines of the scales. Ventral to the lateral band there is no pigment, but a slight silveriness. Microscopic examination shows that the dorsal pigment is confined to the superficial layer of the skin, beneath the epidermis; it consists of black chromatophores, with very little yellow pigment. In this part there is no reflecting tissue either in the form of iridocytes or argenteum. In the ventral region also no iridocytes are seen, the slight silveriness is due to a thin argenteum. The lateral band is due to a very peculiar arrangement of argenteum. The latter is here very thick, and on its inner side are numerous black chromatophores with some yellow pigment, but the strange thing is that the argenteum forms a flattened tube, the width of which forms the bright band. The outer wall of the tube is continuous with the ventral argenteum, and evidently is part of the skin, but in the inner wall only argenteum and chromatophores are seen, no transparent dermal connective tissue. The interior of the tube is occupied by *muscle*, which in the fresh state is seen to be red, while the other muscles of the body are colourless. When a section of the tube is examined a large nerve is seen to run down it close beneath its outer wall, evidently the nerve of the lateral line. But no structure resembling or corresponding to the ordinary tube or sense organs of the lateral line was observed.

In *Osmerus eperlanus* the similar band was found to be due to a special local thickening of the argenteum, and beneath it the muscle was brownish, but the argenteum does not form a tube enclosing a separate lateral muscle, as in *Atherina.*

(*b.*) *Histology.*

It is generally believed and stated by histologists that pigment in the skin is contained in branched connective tissue cells in all respects similar to those which occur in uncoloured parts of the skin. We are unable either to confirm or deny this, since up to the present time we have not succeeded, in spite of persistent attempts, in demonstrating the cellular nature of the chromatophores. We have cut sections of the skin of the various Fishes examined, and have frequently made preparations by the chloride of gold methods, and by the more modern method of steeping in methylene blue and then fixing with picrate of ammonia. We have so far failed to distinguish the connective tissue cells in the skin, but hope to resume this part of the investigation with more satisfactory results at some future time. The present section merely deals with the minute relations of the coloration elements as seen in sections stained or unstained.

The first fact to be mentioned is that the pigment is not exclusively confined to the derma, but occurs in some cases also in the epidermis. A typical instance of this is afforded by the Flounder where, in any section of the upper side of the skin, black pigment is seen in the epidermis. Coloured pigments are not seen in sections, because they are dissolved out by the alcohol in the process of preparation. The black pigment is not contained as a rule in the epidermic cells but between them, sometimes in masses which resemble in section the chromatophores of the derma, and look as though some of the latter had bodily migrated into the epidermis; more usually the pigment appears in granules or thin short threads, which might be sections of branches of chromatophores. In a specimen of the Fish which had soaked for some months in diluted glycerine the epidermis peeled off in patches of some size, and these, when mounted and stained, showed beautifully the condition of the pigment in this layer. It appeared in the form of somewhat injured chromatophores; there were small spots of pigment often with processes round the circumferences, and in some cases the processes were long and branched like those of normal chromatophores. In other cases the processes were interrupted and broken up into dots, but the particles still presented in their arrangement traces of their derivation from radiating branched processes. Many of the spots of pigment were smaller, mere rounded dots, with no indication of processes. The question of the origin of the pigment in the epidermis will be considered subsequently. Pigment in the epidermis occurs also in the Dab (*P. limanda*) but much less abundantly. Particles of black pigment are occasionally seen in the epidermis of other Fishes when sections are examined, but we have met with no case in which the abundance of epidermic pigment is as great as in the Flounder, and in no case is the pigment in this layer of any importance as a factor in the visible coloration, although its presence is an important fact in relation to the physiological history of the pigment in Fish and in higher Vertebrates.

Of the relation of the "coloured" pigments to connective tissue cells or to other ultimate element of the dermal tissue, we can say still less. In some cases, as for instance the Whiting, there are yellow chromatophores having a radiate dendritic structure and as definite an outline as the black chromatophores. In the Flounder and Plaice, on the contrary, the coloured pigment is in the form of a central darker orange spot surrounded by a halo of light yellow which has no definite outline but fades away gradually at a greater or less distance from the centre. The coloured chromatophores, at least in these Flat Fishes, have to some extent the power of contraction and expansion, like the black. It may be provisionally suggested that the coloured pigment is deposited in connective tissue cells as centres, and that in many cases it diffuses from these centres into the surrounding tissue for some distance. Very often the diffused pigment become continuous over a considerable area. In *Cottus bubalis*, for instance, there is a red pigment which occurs in round dots in stellate chromatopores with short processes, or in a uniform network of fine lines in which it is impossible to distinguish the centres of the several chromatophores, and there is also in addition a yellow pigment which is always diffused; it appears in streaks and areas instead of being uniformly continuous, but it is nowhere possible to distinguish chromatophores formed by it. After the Fish has been dead some time this yellow pigment is often found to have separated itself into small spots, but these do not possess radiating processes or definite outline.

The next point to be considered is the relation of the iridocytes and reflecting substances generally to the cellular elements of the dermal tissue. In sections of the skin of the Flounder from the right or upper side the iridocytes are seen to form a single row close beneath the epidermis; they are thicker than might be expected from the appearance presented by their outer surfaces. The section of each is elliptical, and nearly half as thick as it is broad. There is nothing to show that the iridocytes bear a definite relation to the cellular elements of the dermal tissue; they appear to be rather simple deposits in the interstices of the surrounding tissue. The black chromatophores embrace them closely on the outer side, sending their processes between them, and even beneath them, so that in many places the outline of the section of the iridocyte itself is entirely obscured. The internal structure of the iridocyte itself is not merely finely granular or homogeneous, but appears to consist of parallel plates passing obliquely from the outer to the inner surface.

When the iridocytes are examined in a slice of skin cut parallel to its surface, so that their outer surfaces are seen, a small circular aperture is seen in them. Sometimes it is in the centre, sometimes near the edge, sometimes it is on the edge, and then it is no longer an aperture, but an emargination. Occasionally the emargination of one iridocyte is opposite to that of a neighbouring one, as though the two had recently been formed by the division of a single parent element. All these appearances suggest the idea that the circular aperture is really a nucleus—the nucleus of the original cell in the body of which the opaque substance has been deposited. POUCHET, in fact, speaks of the appearance of the circular aperture as due to a spherical nucleus; he is describing the iridocytes in the skin of the upper side of the Turbot. In the Flounder the iridocytes measure about 10 by 20 μ in breadth and length by 5 μ in thickness.

The section of the iridocyte shows a narrow elongated central space surrounded by the opaque substance, which is transversely striated as though consisting of thin plates placed parallel to one another, and vertical to the surfaces of the element. In superficial aspect the opaque substance is seen to form groups of parallel lines, the direction of each group forming angles with those of other groups. Presumably these lines or rods are the edges of the plates seen in section. POUCHET's description of the same appearance in the iridocytes of the Turbot is as follows:—Within the cells are seen "des corps particuliers oblongs, mesurant 1 sur 2 μ environ, paraissant quelquefois renflés à leurs extrémités, placés les uns contre les autres et affectant par groupes une disposition parallèle dans l'intérieur de la cellule." The same author mentions that on the fins of the Turbot, at the extremities of the rays, the iridocytes, instead of a compact polygonal form, have a branched form, presenting broad processes, which, coming into contact with those of their neighbours, form a net-work. He considers that this structure makes still more evident the relation of the iridocytes to the "éléments du tissu conjonctif," which we presume means the connective tissue cells. The same form and arrangement of the iridocytes occurs also in the skin of the fins of the Flounder, but the processes are scarcely comparable to those of chromatophores or those of ordinary connective tissue cells, so that it is by no means certain that these stellate iridocytes are modifications of the latter. In other Fishes, *e.g.*, *Cottus bubalis*, the reticular arrangement of the reflecting substance occurs in all parts of the skin to the exclusion of separate iridocytes; but in such cases it is by no means evident that the substance is contained in connective-tissue cells. The difficulty of connecting the iridocytes with these cells is still greater in such cases as the Whiting and Herring or Sprat, where the former have the form of short rods or prisms lying side by side in uninterrupted contact. Here there is no appearance which suggests nuclei, and no question of either polygonal or branched bodies suggesting cells. The same remark applies to nearly all the Fish mentioned in this paper, except the Pleuronectidæ, of which family the polygonal regularly arranged iridocytes are characteristic.

Indications of *any* relation to cellular or other histological elements are still less to be seen in the argenteum. It is very tough, so that uninjured sections of it are difficult to obtain. No nuclei appear in it after staining. A circumstance which is probably of some importance in relation to the histology of this layer is that in the Mackerel the black chromatophores which are on its inner or deeper side are not confined to its surface, but their processes penetrate its substance, and some of the chromatophores are imbedded in it.

(*c.*) *Development.*

It is well known that chromatophores, both black and coloured, appear in the development of Teleosteans at a very early age, namely, long before the larva is hatched. The appearance of the chromatophores in the newly hatched Flounder, and up to an early stage of the metamorphosis, when the little Fish is 10·5 millims. long, is figured in my 'Treatise on the Sole,' Plate 17, figs. 3–5. Up to the stage last-mentioned, iridocytes and argenteum are wanting, in fact the reflecting substance in any form is entirely absent, both from the skin and the peritoneum; there may be some in the eye, but that organ is here excluded from consideration. On the other hand, in young Flounders, 15 millims. long, in which the metamorphosis has been completed for some time, iridocytes are present in considerable abundance both in the upper and lower sides, but the argenteum has not yet appeared. On the upper side the iridocytes at this stage are more abundant than on the lower, the converse of the relation in the adult condition; but even on the upper side they are not uniformly distributed, but are crowded together in the neighbourhood of the lateral line, and along the intermuscular septa, absent from large areas in other parts of the skin. On this side also, the iridocytes are more abundant in the region of the body cavity than elsewhere, and beneath the skin in this region plates of opaque substance can be imperfectly discerned, which probably are situated in the peritoneum. On the lower side of the body at this stage, the iridocytes are only present in the region of the fin-muscles towards the anterior end of the body, absent elsewhere; the chromatophores have not entirely disappeared from this side. In a slightly earlier stage, when the little Flounder is only 12 millims. long, but after the left eye has reached the right side of the head, there are no iridocytes on the lower side, except a very few on the ventral border of the operculum, while, on the upper side, they are fairly abundant over the head, the region of the body cavity, and the immediate neighbourhood of the latter, but absent from the rest of the body surface. The development of the iridocytes in the skin begins therefore very soon after the metamorphosis is complete, and takes place at first more rapidly on the upper side than on the lower. At the length of 15 millims. the reflecting substance begins to appear in the peritoneum. The presence of the iridocytes in the skin of the lower side causes no opacity in the appearance when the Fish are examined with the unaided eye in the living or fresh condition; the skin appears translucent, not, of course, perfectly transparent as in the larva. The iridocytes can only be detected by the microscope. As the Fish grows older and larger, a white opaque substance begins to appear, not gradually all over the lower side, but in certain regions. In the experiments described in another section of this paper, the lower sides of the living Fish, from the stage of metamorphosis onwards, were frequently noticed and examined, as seen by reflection in the mirror through the glass on which the Fish rested. The first part to become opaque was the area corresponding to the body cavity; the opacity was confined to this region until the Fish was about 2·1 centims. long. After this the opacity appeared in regions outside this limit, appearing at first along the lateral line and the intermuscular septa, whilst the intermediate areas remained opaque. The opacity then gradually extended over the lower side of the body, becoming uniform and continuous at a length of about 7·3 centims. The development of the opacity does not correspond exactly to the size of the Fish, some becoming uniformly opaque while at a slightly smaller size than others, but it is more definitely related to the size of the Fish than to its age, or any other quality. The specimens in the experiments were all collected at the same time, and differed very little in age. But in their rate of growth the individual variation was very great. For instance, on July 18, 1892, the condition was noted as seen with the unaided eye, of thirty-five specimens reared from the previous spawning season. Only one of them exhibited uniform opacity over the whole of the lower side, it was 7·3 centims. long. Another was quite as large, but the opacity was only partially developed in it chiefly along the lateral line and the septa. The smallest were 2·1 centims. long, and in them the opacity was confined to the region of the abdominal cavity, and the rest were of various intermediate sizes, and various intermediate conditions in respect of this character.

This development of opacity, with dull whiteness of surface, is entirely due to the development of the opaque reflecting substance which is deposited on the inner surface of the skin and in the peritoneum, forming the argenteum. As was stated above this substance begins to appear in the peritoneum first, namely, when the Flounder is 15 millims. long. It causes here a uniform opacity, being developed equally in all parts, not along certain lines as in the skin. Careful microscopic examination shows that for some time after the reflecting substance has appeared in the peritoneum, there is none on the internal surface of the skin; the opacity of the abdominal region at this period is due only and entirely to the argenteum of the peritoneum. The latter consists at first of distinct polygonal plates separated from one another by thin transparent lines, and reminding one of the tiles of a tesselated pavement, or the divisions of a map. These plates are much larger than the iridocytes of the skin, measuring ·04 to ·05 in their longest diameter, and ·02 to ·03 in their shortest. The outlines of these plates are very sharp and definite, but the shape is variable, no two being exactly alike. They resemble the iridocytes of the outer layer of the skin in appearance, but are more regularly arranged, and more closely approximated. They exhibit like the iridocytes, a transparent nucleus-like spot towards the centre; their structure is finely granular.

The smallest specimens of the Fish in which the argenteum of the inner layer of the skin was detected was 5·6 centims. long. Here the deposit, like that of the peritoneum just described, consisted of polygonal plates placed edge to edge, and separated by thin transparent lines. The longest diameter of the largest of these plates was ·02 to ·03 millim. while the longest diameter of the iridocytes in the outer layer of the skin did not exceed ·01 millim. The deposit was present only over the abdominal region and in the neighbourhood of the lateral line anteriorly, absent over the rest of the lower side of the Fish. In a piece of the skin examined after being mounted entire and unstained in Canada balsam the plates exhibited the same structure as the superficial iridocytes. There was a clear spot resembling a nucleus, and the rest of the plate exhibited groups of parallel lines, some in one direction, others in others. In this specimen the peritoneal argenteum still showed a division into separate plates, but the division was less distinct than in the earlier stage described above, and no clear spot could be seen in the plates; it was evident that the originally distinct plates were coalescing into a continuous deposit. In section the plates at the inner surface of the skin exhibited a structure quite similar to that of the iridocytes near the outer surface, namely, a striated structure, the striæ being in close juxtaposition and obliquely transverse to the long diameter of the section.

The first traces of the argenteum on the inner surface of the skin of the lower side are well seen in preparations from young Brill 8 and 9 centims. long. In transverse sections the similarity of structure between the iridocytes of the outer level and the inner level is well seen. The differences are these: the external bodies are smaller, more numerous, and more uniformly distributed; while the internal are larger and fewer, several of them occurring in close proximity in one place, none at all in another. The transverse striæ described in the Flounder are well marked in the Brill both in the internal and external bodies. In a piece of the skin mounted flat in Canada balsam unstained the two layers of iridocytes can be separately seen by focussing at the corresponding levels. The distribution of the outer is related to that of the scales, they are more numerous over the central regions of the exposed portions of the scales, scarce along their borders. On the other hand, the deeper iridocytes which belong to the argenteum are arranged in rows, they are elongated in shape, and touch one another by their extremities; the rows again form a loose net work with irregular meshes.

It is evident from the facts thus elucidated, that there is no difference in kind between the two structures which have been distinguished as iridocytes and argenteum. The argenteum in its primitive condition in the Flounder is a collection of iridocytes. But no case is yet known in which the superficial iridocytes develop into a continuous layer of argenteum. We cannot say at present why the reflecting substance is abundantly deposited in the skin near both surfaces, and not at all at intermediate levels, nor why the deeper layer often increases till it becomes continuous and of considerable thickness, while the more superficial layer remains always in the form of separate iridocytes.

There are interesting cases, however, in which the argenteum developed at an early period of life diminishes or disappears at a later period. It has long been known that the various species of *Motella,* which in the mature state live at the bottom and hide themselves under stones and in holes and crevices, are in the young state active pelagic little Fishes, living at or near the surface. In the pelagic state they are silvery, in the mature state dark and dull coloured. In a section of a young *Motella tricirrata* 2 centims. long, a thick deposit of reflecting substance is seen in the skin at the sides of the body, it is absent on the back and becomes thinner towards the edge of the belly. This deposit consists of superimposed flat laminæ, and to it is, of course, due the silvery brightness of the little Fish. On the other hand, in a specimen of the same species 21 centims. long not a trace of reflecting substance can be detected either in the form of iridocytes or otherwise, either near the outer surface or at the inner surface. This suggests a relation between the presence of the reflecting substance and the conditions of life of the Fish, which will be more fully considered in another section of this paper.

II.—Chemical Composition and Spectroscopic Properties of the Pigments and Reflecting Substance.

The reflecting substance which composes the iridocytes and argenteum of the skins of Fishes is guanin, the optical properties of which are very remarkable. The presence of guanin in Fishes' skins was first demonstrated by Barreswil and Voit, about 30 years ago. This important physiological fact was reached indirectly by the analysis of the peculiar substance used for the manufacture of artificial pearls. These pearls are made chiefly in Paris from material which goes under the names of "blanc d'ablette" and "essence d'Orient." *Ablette* is the French name for the Bleak, a fresh-water Fish whose specific name is *Alburnus lucidus,* and from the scales of which the substance is prepared. Barreswil[*] examined this substance and found that it was insoluble in water, in ammonia, and in acetic acid, soluble in sulphuric, nitric, and hydrochloric acid; that the salts from these solutions had a characteristic crystalline form; that the sulphuric combination was easily decomposed by water; that the nitric solution, on evaporation, yielded a yellow compound which was transformed by potash to a red substance, that the nitric salt was precipitated by nitrate of silver. In all these, and various other properties the substance resembled the guanin of Bodo Unger, isolated from guano in 1845.

In 1863 Voit published in Von Siebold's 'Süsswasserfischen von Mittel-Europa' a similar conclusion concerning the nature of this substance, called in Germany "Perlenessenz," having examined it without any knowledge of BARRESWIL's work. VOIT deals more fully with the matter in a later communication published in 1865.* In this paper he summarizes the investigations that had previously been made into the nature of the crystals contained in cells in the scales and other organs of Fishes, and determining the metallic lustre of these parts. Besides the material obtained from the scales of the Bleak, glittering crystals from the air-bladder of *Argentina sphyræna* are also used for making artificial or "Roman" pearls. VOIT re-examined both these substances and found in the former guanin and lime; he held that the lime was not in the form of phosphate but was in combination with the guanin. He found that the substance prepared from *Argentina* consisted of guanin somewhat contaminated with fat, but containing no inorganic matter.

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[*] 'Comptes Rendus,' vol. 53, p. 246. 1861.

According to MOREAU ('Poissons de la France,' 1881) the "essence d'Orient" obtained from the Bleak is the silvery substance which clothes the internal face of the scales, and which is formed of small acicular crystals. We have not ourselves examined the Bleak, but it is evident from this description that these acicular crystals correspond in properties and in position with those of the Herring and other Clupeoids. MOREAU adds that to obtain the best product only the ventral scales are taken, because these are free from the greenish pigment which occurs in those of the back.

In 1880 KÜHNE and SEWALL† published an account of their researches upon the eyes of Fishes, especially of *Abramis brama*, the common fresh-water Bream. They found opaque reflecting granules in the retinal epithelium, which were found to consist of pure guanin; but, on the other hand, they found that the brilliant lustre of the argentea of the iris in *Abramis* and other Teleosteans consisted of guanin combined with lime (*guaninkalk*), and they found the same compound in the tapetum of Elasmobranchs, forming the granules called ophthalmoliths by DELLE CHIAJE.

The only examination in any detail of the distribution of guanin in various species of Fishes that has preceded our own is that of EWALD and KRUKENBERG.‡ These investigators state that in Fishes, as in Reptiles and Amphibia, the guanin is contained in connective tissue cells, in some cases in fine crystalline plates as a lime compound (*guaninkalk*) (Teleostei, Ganoidei, Cyclostomata), in others in the pure condition, and then it is only dead white, and has no metallic lustre (skin of Selachians). They found it, in the various Fishes examined, in the external skin, the scale-pockets, the subcutaneous connective tissue, the fasciæ of the muscles, in the air-bladder, the gall-bladder, and the peritoneum. The authors point out various peculiarities in the distribution of the guanin in various species. They mention that the ventral skin usually contains more guanin than the dorsal; but that in *Solea*

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* "Ueber die in der Schuppen und der Schwimmblase von Fischen vorkommende irisirende Krystalle," 'Zeitsch. f. wiss. Zool.,' vol. 15.

† 'Untersuch. a. d. Physiol. Inst. Heidelberg,' vol. 3, p. 221.

‡ 'Zeitschrift f. Biologie,' vol. 19, p. 1, 1883.

platessa, which probably is a misnomer for the Plaice, the darker surface turned towards the light is much poorer in this substance than the whitish lower side. They remark that the Mackerel and *Caranx trachurus* are also exceptions to the rule, the external blackish or steel-blue parts of the skin in these Fishes containing considerable quantities of guanin. It will be seen from the description we have given of the distribution in the Mackerel that this is a mistaken conclusion, the guanin in the subcutaneous argentea being more abundant ventrally than dorsally, while the quantity in the outer layers of the skin is comparatively insignificant. The authors point out that there is no constant relation between the quantity of guanin present in the peritoneum and the quantity in the skin; in *Zeus faber* the substance is pretty equally present in both, while in *Cepola rubescens* the peritoneum is rendered brilliantly silvery, and the skin, except on the head, contains no guanin at all.

Few observations have been made on the pigments of Fishes' skins. The most remarkable of them are those of GEO. FRANCIS,* described in a letter to 'Nature' in 1875. According to these observations, which have never been confirmed, the blue-green colour of certain brilliant Fishes, living in St. Vincent's Gulf, South Australia, namely, *Odax radiatus*, *O. frenatus*, *O. Richardsonii*, and *Labrichthys Richardsonii*, is due to a pigment which is soluble in water and in sea-water, but destroyed by heat, chlorine, acetic acid, ammonia, and alcohol. Sulphuric acid precipitates it, but does not destroy it. Its spectrum resembles that of chlorophyll. Both *Odax* and *Labrichthys* belong to the family Labridæ, or Wrasses, of which nearly all the members are brilliantly and conspicuously coloured, especially the tropical forms. No observations on any species of Wrasse are included in the present paper.

KRUKENBERG† has examined the red pigment of the tail of *Luvarus imperialis*, which he found to be situated in the form of granules in the epithelial cells (epidermis), and to be tetronerythrin (or zoonerythrin), a distinctly characterized pigment belonging to the class of lipochromes, and found in diverse divisions of the animal and vegetable kingdoms. He also‡ examined the pigments of *Cyprinus auratus*, *C. carpio*, *Barbus fluviatilis*, *Muræna Helena*, *Belone rostrata*, *Scorpæna scrofa*, *Solea vulgaris*, and *Mullus barbatus*. He found tetronerythrin in *Cyprinus auratus*, the gold-fish; also in *Cyprinus carpio*, mixed with a yellow lipochrome. In the other species he found lipochromes differing from each other occasionally in minor points. He failed to isolate or even to obtain in solution the peculiar green pigment from the scales, bones, &c., of *Belone rostrata*. Some years ago Professor RAY LANKESTER§ examined *Belone*, and also the Mackerel, Wrasse, Red Mullet, &c., with a negative result as regards absorption bands.

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* 'Nature,' vol. 13, p. 167.

† 'Vergl. Physiol. Studien,' 1te Reihe, 4te Abth., 1881, pp. 32–37.

‡ '*Ibid.*, 2te Reihe, 2te Abtheil., 1882, and 3te Abtheil., 1882.

§ 'Journ. Anat. and Physiol.,' 1869, p. 119.

The general results of our own observations are as follows. The only pigments found in the skin were lipochromes and melanins, and neither could be obtained pure. A striking uniformity is perceptible in the wave-length measurements of the absorption bands of solutions of the lipochromes of allied species. For instance, in the Pleuronectidæ (see Table, p. 787) with the exception of those from *Arnoglossus megastoma*, all the measurements agree closely. Even in Fishes of widely separated species a close agreement in the position of the bands is apparent from the Table. Other points of interest are brought out by the Table; thus we see that the colour is of less importance in determining identity than the position of the bands. Here it may be remarked that inspection of a skin with the naked eye, or even with the microscope, may lead one to suppose that two pigments are present, for instance, a yellow and a red, but, on spectroscopic examination, it is found that the red colour is due to greater concentration of the same pigment, which in thin layers may be yellow, and in thick, red. Sometimes, however, two pigments, a yellow and a red, may be present. It is found when such is the case, as in *Nerophis æquoreus*, *Cottus bubalis*, and *Pleuronectes flesus*, that the yellow can be separated from the red by first extracting the skin with alcohol, and then with ether, the former taking up the yellow pigment, the latter the orange or red.

The fact ascertained by KRUKENBERG that the pigment of the Gold Fish, *Carassius auratus*, is tetronerythrin was confirmed, and the same pigment was found in the fins of *Trigla cuculus*, but not in the skin of the body, which contained another red lipochrome. The residue left by evaporation of the lipochrome solutions always gave a blue or green coloration with nitric and sulphuric acids, but gave no marked reaction with iodine in potassium iodide, although sometimes the reaction was obtained by using SCHULTZE's fluid. This negative result with iodine is often noticeable in the case of animal lipochromes.

In all cases the melanins, the pigments contained in minutely granular form in the black or brown chromatophores, were found to be very refractory towards solvents. No connection could be traced between the lipochromes and the melanins, and in the integument of a young *Alligator Mississipiensis* which showed a yellow and a black pigment the yellow was found not to be a lipochrome, so that here at least the melanin could not have owed its origin to a lipochrome.

The muscles of Fishes, as is well known, contain but little hæmoglobin. But in one or two cases it was found in such a position as to have some effect on the external appearance. In *Arnoglossus megastoma* some reddish spots visible through the integument were found to be due to hæmoglobin in the underlying muscle. In the tubular lateral silvery band of *Atherina presbyter* the enclosed muscle was found to be coloured by hæmoglobin, in places replaced by myohæmatin. In *Osmerus eperlanus* the argenteum of the lateral band is not tubular, but the muscle beneath the band is coloured by myohæmatin, limited to the breadth of the band.

The beautiful metallic appearance of the iris in Fishes is due to crystals of guanin.

This so-called argentea was examined microscopically and chemically, and wherever a silvery argentea was present, crystals of guanin were accountable for the appearance, while, where a golden appearance, as in *Trigla hirundo*, was seen, a yellow or orange lipochrome was found deposited over the guanin layer (*vide* Plate 55, fig. 12). The crystals of guanin in the argentea of the eye occur as fine needles arranged in sheaves. The guanin may easily be obtained by extracting those parts which contain it with dilute hydrochloric acid. It can be obtained as crystals by adding ammonia to the solution, but the crystals are very small and easily pass through filter paper. The silvery peritoneal layer, the silvery air-bladder, the subcutaneous reflecting layer, or argenteum, the white or silvery parts of the skin, and the argentea of the eye, all owe their appearance to guanin. The iridocytes in the skin of Flat Fishes, and the iridescent prismatic crystals in that of others, are composed of guanin. If dilute hydrochloric acid be allowed to run beneath the cover-glass, the crystals melt before it, and the guanin disappears. If the solution in this acid be evaporated down, and the residue dissolved in strong nitric acid and evaporated again over the free flame to dryness, a yellow residue is obtained which, when touched with caustic soda solution, becomes red; heated, becomes purple. To prove whether calcium is present with the guanin, as has often been stated, apparently on insufficient evidence, the guanin was dissolved out of the air-bladder of the Herring with dilute hydrochloric acid. The air-bladder contains no crystals of calcium phosphate as the skin often does. The solution of guanin was evaporated to dryness, the residue incinerated, and the ash treated with sulphuric acid on a glass slide under the microscope. Not a single crystal of calcium sulphate was obtained. But it was noticed in the course of these observations that very large prismatic crystals occur in the skin of many Fishes, *e.g.*, *Pleuronectes microcephalus*, *P. limanda*, *Arnoglossus megastoma*, *Cottus bubalis*, *Solea variegata*, *Clupea harengus*, *Trigla gurnardus*, reminding one of the crystals of ammonic magnesium phosphate met with in urine. These dissolve in dilute hydrochloric acid, and by the usual tests it was proved that they are composed of calcium phosphate. In *Solea variegata* some of these large crystals measured as much as 106 μ by 29 μ, in *Arnoglossus megastoma* 264 μ by 96 μ, down to 36 μ by 12 μ.

No sufficient evidence is available on the question of the extent to which guanin deposits occur as elements of coloration in the skins of Invertebrates; EWALD and KRUKENBERG* state that the spindle-shaped crystalloids in the brilliant silvery sklera of *Sepia officinalis* and *Loligo vulgaris* do not consist of guanin, and that it is likewise absent from the iridescent skin of these and other Cephalopods (*Sepiola Rondoletii*) which owes its metallic appearance to the fine striation of the cells. We have, however, demonstrated that in one Invertebrate chalk-white markings in the skin are due to guanin. *Antiopa cristata* is a beautiful Nudibranch Mollusc with a number of dorsal papillæ. Each papilla has a conspicuous chalk-white tip, and there are similar opaque white patches on the skin of the body. Under the microscope these marks were found to consist of iridescent granules in the skin, and these granules were found to be soluble in caustic potash and in hydrochloric acid. The solution in the latter responded to the guanin test with nitric acid and caustic soda.

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* 'Zeitsch. für Biologie,' vol. 19, p. 1, 1883.

We proceed now to give the details of our observations on the skins of Fishes from the chemical and physical point of view.

Pleuronectes flesus—the Flounder. A greenish part of the skin shows, in ZEISS' microspectroscope, a shading from about λ 485 to λ 515, but it is very indistinct. Extracted with alcohol, the skin yielded a yellow solution, in which a band is dimly seen, from about λ 496 to λ 475. The yellow residue left on evaporation of this solution was soluble in chloroform, the solution showing a band from about λ 504 to λ 477; in bisulphide of carbon with a band from about λ 526 to λ 499, and in other lipochrome solvents. An ether extract of the skin was of a deeper yellow and left, on evaporation, an orange lipochrome which was soluble in the usual solvents, and gave the usual reactions in the solid state. The measurements of the bands of the solutions are given in the Table.

No crystals were observed in the skin in this species. In the argentea of the eye, which round the margin of the pupil is slightly golden, guanin occurs in needles arranged in bundles, over which an orange-red lipochrome is deposited.

Pleuronectes platessa—the Plaice. Although one would expect to find two lipochromes in the integument of this species only one could be extracted, which was of a yellow colour. The red appearance of the pigment in the centres of the chromatophores is apparently due to greater thickness of the deposit. The solutions of the lipochrome showed only one band, the measurements of which are given in the Table.

Pleuronectes limanda—the Dab. The skin contains a comparatively small amount of yellow pigment. Only one lipochrome of a yellow colour, with a greenish tinge, was extracted by solvents, and was evidently identical with, or closely related to, the orange one found in *P. flesus*, as can be seen by consulting the Table. Why a yellow pigment from one fish should appear to be identical spectroscopically with a more orange coloured one in another is not clear. It would seem that mere colour is of less importance than spectroscopic characters.

Besides the iridocytes very minute crystals of guanin are found at the surface of the skin and exceptionally a large prismatic crystal of calcium phosphate.

In *Pleuronectes microcephalus*, the Merry Sole, as it is called at Plymouth, are found in the skin large prismatic crystals which respond to the tests for calcium phosphate. The coloured pigment, or lipochrome, yields a yellow solution, of which the bands are given in the Table.

In *Solea variegata* a yellow and a red pigment are seen in the coloured chromatophores, but only one pigment could be extracted (see Table of wave-lengths). Large and small prismatic crystals occur abundantly, the former consisting of calcium phosphate (fig. [illegible]), the latter probably of guanin.

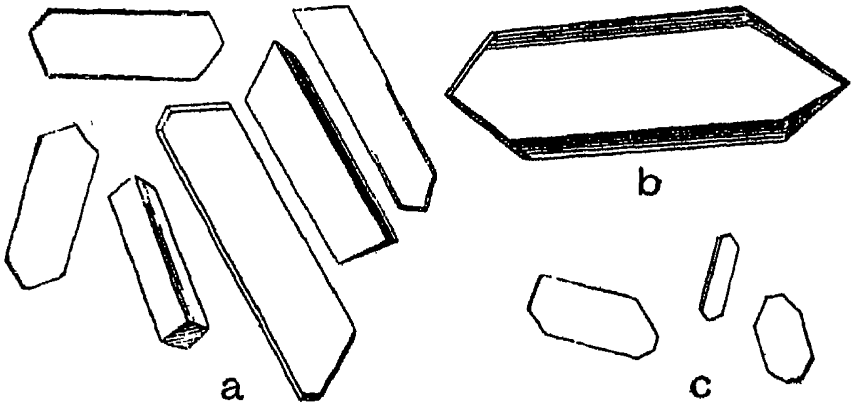
TABLE of Wave-length Measurements of Absorption Bands of Solutions of Lipochromes in Skins of Fishes.

(In millionths of a millimetre.)

	In ether.	In chloroform.	In carbon bisulphide.	Colour.
Pleuronectes flesus	494 — 471 458 — 441	504 — 477 467 — 450	520 — 494 488 — 467	Orange
Pleuronectes platessa	496 — 471	504 — 475	..	Yellow
Pleuronectes limanda	494 — 467 458 — 441	501 — 477 464 — 446	509 — 483 471 — 453	Orange yellow
Pleuronectes microcephalus	496 — 469 455 — 438	501 — 475 466 — 448	517 — 494 488 — 467	Yellow
Solea variegata	493 — 469 460 — 445	501 — 477 466 — 448	523 — 496 490 — 469	Reddish
Arnoglossus megastoma	483 — 464 451 — 435	496 — 473 462 — 444	..	Orange yellow
Trigla cuculus	481 — 460 448 — 432	490 — 469 455 — 438	509 — 485 473 — 455	Orange
Trigla hirundo	481 — 462 450 — 433	494 — 471 460 — 443	509 — 488 473 — 456	Orange
Trigla gurnardus	479 — 462 448 — 432	491 — 469 462 — 444	506 — 485 473 — 455	Yellow
Cottus bubalis	499 — 475	501 — 475	..	Yellow
Cottus bubalis	481 — 462	496 — 469 460 — 443	511 — 488 477 — 458	Reddish
Scomber scomber	477 — 458 448 — 432	488 — 469 457 — 440	504 — 481 469 — 451	Yellow
Syngnathus acus	477 — 458 448 — 432	490 — 467 458 — 442	506 — 483 473 — 455	Orange yellow
Siphonostoma typhle	479 — 460 446 — 430	492 — 469 458 — 442	506 — 485 471 — 453	Greenish yellow
Nerophis æquoreus	479 — 460 446 — 429	490 — 467 457 — 440	511 — 488 475 — 457	Reddish
Nerophis æquoreus	494 — 469	496 — 473	..	Yellow
Clupea harengus	481 — 462 450 — 435	492 — 471 460 — 443	511 — 485 473 — 453	Yellow
Atherina presbyter	479 — 460 448 — 432	490 — 469 460 — 445	509 — 485 471 — 453	Yellow
Osmerus eperlanus	492 — 467 458 — 442	501 — 477 467 — 450	523 — 496 490 — 469	Yellow
Zeus faber	479 — 460 448 — 432	491 — 469 460 — 445	509 — 485 471 — 453	Yellow
Gasterosteus spinachia	481 — 460 446 — 430	492 — 471 460 — 443	511 — 485 473 — 453	Reddish yellow
Carassius auratus	506 — 473	520 — 477	Shading at 552 517 — 483	Red

The light brown skin of *Arnoglossus megastoma* exhibits some reddish spots which were found to be due to deposits of hæmoglobin in the underlying muscle, so that here hæmoglobin plays a subordinate part in the coloration of the skin. The melanin is not abundant, an orange-yellow lipochrome is extracted by solvents. The large prismatic crystals (*b*, fig. 1), abundant in both the coloured skin of the upper side and the white of the lower, are composed of phosphate of calcium.

Fig. 1.



Large prismatic crystals of Calcium phosphate from the skins of various Fishes: *a*, from Solea variegata; *b*, from Arnoglossus megastoma; *c*, from Clupea harengus.

Trigla cuculus.—The presence of guanin in the reflecting layer, in the white skin, and in the argentea of the eye was determined by the usual tests. Spherical crystals, reminding one somewhat of leucin, which occur at the surface of the skin, consist of radiating needles of guanin. Under the microscope the red pigment in round chromatophores and the diffused yellow pigment appear very distinct. Under ZEISS' microspectroscope the reddish integument gave a band from λ 480 to λ 505. The alcohol extract of the skin was pale yellow and showed no band; on evaporation a pale yellow residue was left which was soluble in chloroform, the solution showing no noticeable band. On the other hand, an ether extract, while up to a certain depth it simply absorbed the violet end of the spectrum, to λ 520, when more concentrated showed two bands, the measurements of which, with those of the other solutions, are seen in the Table. This lipochrome responded to the usual tests and was orange-red in colour.

The fins, on the other hand, contain tetronerythrin, the ether solution of which was of a fine red colour and strongly absorbed the violet end of the spectrum. In a diluted solution a broad shading became detached in the green from about λ 517 to λ 464. The residue from the solution was of a brilliant red colour and soluble in the usual lipochrome solvents. It became dark green, when touched with a drop of SCHULTZE's liquid, dark blue with nitric acid, blue and blue-green with sulphuric acid. This tetronerythrin occurs in definite chromatophores in which granules are apparent.

Trigla hirundo.—The reflecting layer contains very small prismatic crystals of guanin—looking like bacteria. The argentea of the eye has a golden appearance, caused by the presence of guanin in needles arranged in bundles, above which an orange-coloured lipochrome occurring in granules and oil-globules can be seen in Plate 55, fig. 12. No crystals of calcium phosphate were detected.

The skin under the microspectroscope showed a band from λ 480 to λ 505, belonging to a lipochrome which readily dissolved in ether and the usual solvents, but alcohol extracted only the merest trace of pigment. This lipochrome in solution is gamboge yellow, and gave the usual reactions with nitric and sulphuric acids, but not with SCHULTZE's liquid.

Trigla gurnardus.—In addition to the usual elements large crystals are present, found to consist of phosphate of calcium. Under the microspectroscope the skin showed a band from λ 480 to λ 505, as in the preceding species. Extracted with alcohol it yielded no pigment; with ether it gave a yellow lipochrome soluble in the ordinary solvents, and giving the usual reactions with nitric and sulphuric acids, but not with SCHULTZE's liquid. For measurement of the bands see Table. Here, as in the preceding species, only one lipochrome could be detected by extraction, although under the microscope two distinct pigments seem to be present. The skin, the reflecting layer, in which the guanin occurs in small needles, and the argentea in which it is also seen as needles, all gave the guanin reaction distinctly.

Cottus bubalis.—Two lipochromes can be extracted from the skin, doubtless corresponding severally to the two pigments seen *in situ.* The spectroscopic bands of the two, one yellow in solution, the other reddish, are given in the Table. Guanin was detected in the various parts of the skin examined, and is to be referred to the network of reflecting substance. The large prismatic crystals which occur in the skin gave the reactions of phosphate of calcium.

From the skin of the Mackerel, *Scomber scomber,* a yellow lipochrome was obtained, corresponding to the yellow pigment described *in situ,* giving the bands indicated in the Table. When portions of the silvery reflecting layer or argenteum were dissolved in dilute hydrochloric acid, the solution evaporated, the residue incinerated, and the ash tested on a glass slide under the microscope with sulphuric acid, no calcium sulphate crystals could be seen. The substance consisted of guanin, not combined with calcium. In all parts of the skin, as well as in the reflecting layer, the guanin reaction was easily obtained.

The skin of *Syngnathus acus* yielded an orange-yellow lipochrome, corresponding to the orange pigment seen *in situ* (see Table). Guanin corresponding to the scanty reflecting substance was found.

The skin of *Siphonostoma typhle,* under ZEISS' microspectroscope, showed a band from about λ 480 to λ 505. The slight spectroscopic difference between the single lipochrome of this species and that of the preceding is seen in the Table. The skin contains guanin, of which, also, the peritoneal argenteum consists.

The skin of *Nerophis æquoreus,* the banded Pipe Fish, gives under the microspectroscope a band between λ 480 and λ 510. In the dorsal fin, a red lipochrome, giving a dull band in the green, occurs in chromatophores which are shown in Plate 55, fig. 7.

On extraction with ether, a lipochrome is obtained which gives nearly the same measurements as that of other Pipe Fishes. Besides this, traces of another yellow lipochrome were extracted by alcohol. Attempts were made to extract the melanin from the skin of this and other Pipe Fishes, but it was found extremely refractory towards solvents; its solution in caustic alkalies showed no absorption bands.

In the peritoneal argenteum, the guanin occurs mostly in granules which respond readily to the usual guanin reactions; besides these granules, abundance of crystals occur, whose form is best made out with a power of 800 diameters; they are triangular, with the apex of the triangle removed, and measure from 7 μ in their long diameter to 5 μ, and from 5 μ in their short diameter to $2\frac{1}{2}$ μ. Guanin was also detected in various parts of the skin.

Clupea harengus.—The greater part of the skin is free from yellow pigment, though containing abundance of oil in colourless drops. The dorsal part of the skin under the microspectroscope gave a band from λ 480 to λ 510, and it yielded to ether a yellow lipochrome soluble in the usual solvents (see Table). The argenteum and the iridocytes on the inner sides of the scales were tested and found to be guanin. Under the microscope the needles of the argenteum are seen to dissolve before hydrochloric acid, and in the resulting solution no calcium could be detected. The silvery appearance of the air-bladder is also due to a layer of guanin in long needles. When a portion of the air-bladder is placed in dilute hydrochloric acid, the silvery appearance soon disappears, more quickly if heat be applied. On evaporating such a solution, and incinerating the residue, no calcium could be detected by microchemical reactions. A mere trace can be detected when present by the formation of calcium sulphate crystals on the addition of sulphuric acid. Very fine crystals can be obtained by taking a solution of the guanin of the air-bladder in dilute hydrochloric acid, neutralizing with ammonia, and filtering off the precipitate. Examined with a $\frac{1}{12}$th immersion objective the crystals appear as in Plate 55, figs. 13 and 14, *i.e.*, in minute spherical crystals and in prisms.

Large prismatic crystals occur on the surface of the scales and in other parts of the skin, and these dissolve in dilute hydrochloric or strong acetic acid; the solution tested for calcium and for a phosphate gave a positive result.

In the dorsal region of *Atherina presbyter* occurs a yellow lipochrome, of which the bands are indicated in the Table. The reflecting substance, the peculiar arrangement of which has been described, is of course guanin. The colouring matter of the muscle enclosed in the cylinder of reflecting tissue is hæmoglobin, which is absent from the other muscles of the Fish. In some places the hæmoglobin is replaced by myohæmatin. The guanin in the argenteum is in the form of needles and prisms. When dilute hydrochloric acid is allowed to act on these the silveriness and iridescence disappear, the crystals dissolve, and others soon appear, which are larger and which give the [illegible] reaction; they are probably formed by partial solution of aggregates of the prisms. Guanin crystals in the form of fine needles are present in the argentea of the eye. The yellowish pigment in the dorsal skin is a lipochrome, whose absorption bands are given in the Table.

The muscle beneath the silvery band in *Osmerus eperlanus*, the true Smelt, gave the spectrum of myohæmatin instead of hæmoglobin. The lipochrome extracted from the skin was also different from that of *Atherina*, as seen in the Table. In the pigmented dorsal region of *Osmerus* crystals of guanin are present in the superficial layer of the skin (iridocytes). They are of irregular shape, and appear green by reflected, red by transmitted, gas-light.

In *Zeus faber*, the John Dorey, guanin forms the argenteum, and also occurs sparingly in the superficial layer. The lipochrome is also in small quantity.

There is an orange lipochrome in the fifteen-spined Stickleback. Its measurements are given in the table.

In the Gold Fish, *Carassius auratus*, the melanin which usually occurs in black chromatophores is absent from part or all of the skin. Iridescent prismatic crystals of guanin occur in contact with the scales; and also beneath the skin is an argenteum, which is thickest on the ventral surface. The specimens of the Fish examined were all golden-red, and no black chromatophores were found in them. Under the microspectroscope the red pigment *in situ*, which sometimes appears to form chromatophores, but is more usually diffused, absorbs the violet end of the spectrum, and gives a broad, ill-defined double shading in the green. All the solutions of the pigment strongly absorb the violet of the spectrum, and give ill-defined bands, whose position is indicated in the Table. The pigment on evaporation is orange red, becomes an evanescent blue with nitric acid, dark green and blue, passing into brown, with sulphuric acid, and remains unchanged with SCHULTZE's solution. The muscles contain hæmoglobin, most plentifully in the dorsal region.

III.—THE ARTIFICIAL PRODUCTION OF PIGMENT ON THE LOWER SIDES OF FLOUNDERS.

The first experiment with living Fish made in this investigation was described in the 'Zoologischer Anzeiger,' No. 354, 1891. We will briefly recapitulate the details here.

Experiment 1.—About fifteen or sixteen larval Flounders, in process of metamorphosis, were used. The apparatus employed was a small glass vessel, cylindrical in shape, with a flat bottom, and about 12 inches in diameter. The sides of the vessel were covered externally with black paper, and an opaque cover was kept over the top. The water in the vessel was kept at a constant level by means of a siphon, which connected it with an overflowing bottle, clean water being supplied by a jet passed through a hole in the cover. Beneath the small aquarium was fixed a mirror, inclined at an angle of 45° to the plane of a south window, opposite which the apparatus was placed. The young Flounders, when placed in this apparatus on May 8, 1890, were

11·5 to 12·7 millims. in length, and their metamorphosis was far from complete. The new conditions to which they were subjected produced no apparent change in the course of the metamorphosis. The eyes passed into the normal adult position, and the colour disappeared at first, as far as could be seen, from the under side as usual. A specimen taken out on June 21, and carefully examined, was 2·7 centims. long and completely metamorphosed; there were no chromatophores on the lower side, except a few widely scattered on the lower side of the head. The little Fish in this experiment were not continuously exposed to the reversed conditions in relation to light which it was intended to produce, for it was observed that they frequently clung to the sides of the vessel instead of lying on the bottom, and, of course, in the former position no light could reach their lower sides.

On Aug. 27, all the Fish died from an accident to the circulation in the tank. There were thirteen of them altogether, ranging in total length from 3·2 centims. to 6·3 centims. In three of them there was a striking development of pigment in a broad band at the edges of the lower surface, the pigment being in the form of black and yellow chromatophores, exactly similar to those on the upper side. In two specimens no pigment was found on the lower side. In the remaining eight there was some pigment in one part or another of the lower surface, but only in small areas or in scattered chromatophores.

Experiment II.—The young Flounders used in Experiment I. were some of a large number, several hundred, which were received from Mevagissey between May 3 and May 8, 1890. The rest of these specimens were placed in table tanks at the bottom of which was a layer of sand, and in these they were fed regularly, and carefully reared. Excepting the confinement, these Flounders were living under normal, natural conditions, burying themselves in the sand when alarmed. On Sept. 17, 1890, four of these specimens were taken and placed in the apparatus used in Experiment I. These Fish were not actually measured, but are known, from records of the size of specimens of the same lot, to have been at that date from 7 to 9 centims. in length. They were about six months old, for, when obtained at the beginning of May, they must have been four to six weeks old. Their metamorphosis was, of course, completed in June; and, at the commencement of this experiment, they were in all respects normal specimens, with the characters of the adult. There was no pigment, no chromatophores on the left or lower side of any of the specimens; but the white, opaque layer, or argenteum, was fully developed on the whole of that side. At the commencement of this experiment the black paper was removed from the sides of the glass jar in which the Fish were placed, but the cover, which was lined with black velvet, was left on the top of the jar. In consequence of this change, light could pass through the sides of the jar as well as through the bottom from the mirror, but not through the top. The Fish now did not cling to the sides much; they seemed to have no preference for that position when the sides were no longer black and opaque. On [illegible] light passing through the sides fell obliquely on the upper sides of the Fish, so that the lower sides were not exclusively exposed to light. The mirror was arranged as before. These four specimens were kept in this apparatus until the beginning of February, 1891, when it was replaced by a shallow wooden tank with a bottom of plate glass. The dimensions of this tank were 3 feet 6 inches in length, 2 feet in width, and 10 inches in depth. The four Flounders were transferred to this tank, and a mirror of corresponding size was placed underneath it. The sides of the tank were black, and a cover was placed over the top, but this cover did not fit with sufficient accuracy to prevent light absolutely from entering above.

On March 10, it was noted that there was as yet no pigment on the lower sides of any of these four specimens, with the possible exception of the smallest. That is to say, if there was any pigment at all in the skin of the lower side of the smallest specimen, it consisted of only a few scattered chromatophores, the presence of which could not be determined with certainty without taking out the specimen and examining it with the lens or microscope—a proceeding which would have endangered the life of the specimen.

On April 26 were noticed two faint specks of pigment on the lower side of one of these specimens.

On July 1 one of the four specimens died, having got fixed between the side of the tank and one of the bricks placed inside the tank to keep the Fish in the central area of the glass bottom. This specimen had no pigment on its lower side. After they were put into the wooden tank these four Flounders followed the usual objectionable habit of clinging to the sides of the tank, instead of lying on the glass bottom with their lower sides exposed to the light. The water in the tank was kept as low as possible, but, while their breadth was small, could not be kept shallow enough to prevent the Fish doing this. As they grew larger they were compelled to abandon the habit, because, when they practised it, part of their bodies were out of water. At this date the smallest still retained this habit, but the other two remained usually horizontal. On one of these the pigment first seen on April 26 had increased a good deal in quantity, and a few specks had appeared on the others.

On August 6 the three remaining specimens were carefully examined, and the following is the entry in Mr. CUNNINGHAM's diary of that date :—" The largest of the three Flounders has pigment all over the external regions of its lower side; the second has scarcely any pigment, but has, I think, started to develop it, at least, it has slight indications of it here and there. The smallest specimen has very little. These two, until within the last few weeks, constantly clung to the side of the tank in a vertical position; the smallest often remains in this position now, but the others cannot do so because they are too large and the water is too shallow."

On September 26 one of the three remaining specimens was found dead behind one of the bricks. It was 16·7 centims. in length (6·6 inches). There was a little pigment on the posterior part of the operculum of the lower side, but nowhere else on that side

The two remaining specimens in this experiment continued to live for several months, and their lower sides were now constantly exposed to the daylight reflected upwards from the mirror, as they were now too large to cling to the sides. In November one of them, that in which pigment began to appear in April, and was first noticed on April 26, was pigmented over almost the whole of the lower side. On November 13 Miss WILLIS commenced to make a water-colour painting of this specimen from life, as it appeared by reflection in the mirror against the dark interior of the tank, and this painting is faithfully reproduced in Plate 53. The other specimen at this time was not pigmented to the same extent, nor, on the other hand, was it entirely destitute of pigment: it had three or four small spots scattered over the region of the abdominal cavity: these spots were not isolated chromatophores, but definite coloured spots, 1 to 2 millims. in diameter. The pigmented specimen figured was 22 centims. long at the time the drawing was made, the other specimen being about the same size.

During the following months the pigmentation of the lower side of these two specimens increased somewhat in area and intensity, but only very gradually. The pigment on the spotted specimen remained in separate spots, and never became continuous. On March 2, 1892, I examined the specimens to see if they were sexually ripe, as they were then 2 years old, and some specimens of the same age in the ordinary tanks were in spawning condition. I found that both were male and both ripe, ripe milt exuding from both on very slight pressure. I used some of the milt to fertilize the eggs of an ordinary Flounder of the same lot, which had been reared in an ordinary tank, but the eggs, although ripe, were not healthy, and all died.

The specimen with separate spots of pigment on the lower side died at last on July 4, 1892. The immediate cause of death was not evident, but a few days before there had been difficulties with the general salt-water circulation of the aquarium, and these two Flounders had been found several times gasping for want of oxygen. The apparatus had been provided with a constant supply of water in the main laboratory, and the Fish seemed to have recovered, but the death of this one was probably due to the after-effects of the crisis. A careful record was made of the distribution of pigment-spots on the lower side of this specimen. It was 23 centims. in length. There was pigment at the edge of the lower side, between the base of the pelvic fin and the ventral angle of the operculum; on the area covered by the pelvic fin; three spots on the area covered by the pectoral fin; seven spots, each 5 millims. in diameter, and several smaller ones, on the ventral half of the side in the neighbourhood of the posterior border of the abdominal cavity; eight minute spots on the dorsal half of the side; about eight spots close to the lateral line on both sides of it; four spots, about 5 millims. in diameter, on the lower surface of the ventral fin; a good deal of pigment over the posterior two-thirds of the lower surface of the caudal fin. The pigment on the upper or right side of the Fish was not appreciably diminished.

The other and last-surviving specimen continued to live in good health; on July [illegible] pigmented area as compared with that shown in the Plate was darker and more extended, reaching quite to the borders of the head anteriorly, and narrowing considerably the white band along the lateral line posteriorly; the patch on the head was also much larger.

This experiment is in some respects the most important and interesting of all those described in this paper. It proves in the most absolute and conclusive manner that normal pigmentation is produced by the incidence of daylight on the under sides of Flat Fishes which have lived for the first six months of their lives under normal conditions, and are at the end of that period perfectly normal specimens in all respects with no trace of pigment on their lower sides. All the time that the experiment was in progress a large number of specimens of the same age procured at the same time were kept in tanks of the aquarium, supplied with sea water by the same circulation, and were fed with the same food. The only difference in conditions between the two cases was that in one the Fish were living on a layer of sand and only exposed to light coming from above, while in the other the Fish were living on a glass plate beneath which was a mirror to reflect the light upwards. There were ninety specimens surviving in February and March, 1892, of those which had been kept in the ordinary tanks, and of these *only one* had a few small patches of pigment on the lower side. On the other hand, recapitulating the results obtained with the four specimens whose lower sides were exposed to light, we find that—

One specimen lived till July 1, 1891, and was exposed to light from below for 9½ months without developing pigment on the lower side.

The second lived till September 26, 1891, and had then been exposed to light from below for a few days more than 12 months, it had only a little pigment on the operculum of the lower side.

In the third specimen pigment was not noted with absolute certainty till November, 1891, when the light had acted for 14 months. The pigment increased slowly, but surely, in quantity until July 4, 1892, when the Fish died, having been kept under the experimental conditions for 1 year and 9½ months. The pigment when the specimen died was still in separate patches, not continuous.

In the fourth specimen pigment first appeared at the end of April, 1891, after the light had acted for a little over 7 months; by August 6, *i.e.*, in the eleventh month, there was pigment extending continuously all over the external regions of the lower side. In November the pigmentation was increased to the extent shown in the Plate, and in the following July after 1 year and 10 months, there was very little unpigmented surface left on the lower side.

Experiment III.—Only a single specimen was concerned in this experiment.

On April 4, 1891, was found in the table tank containing a number of those collected in the larval stage in May, 1890, a Flounder, 15 centims. long, in which there was a single spot of pigment on the lower side, on the area covered by the pectoral fin. This specimen was placed in the glass-bottom tank, and pigment developed on its lower side with extraordinary rapidity. It did not spread from the original pigment spot, but appeared as usual towards the centres of the halves of the surface divided by the lateral line.

On July 12, this specimen was found dead, having killed itself by falling between the bricks and the side of the tank. At the time of death it had pigment over the whole of the lower side except the head and a narrow strip along the lateral line. This specimen in fact after only 3 months' exposure exhibited more pigmentation than the specimen represented in Plate 53, that is to say pigmentation which extended over a greater area, although it was not quite so dense, and therefore not so dark in colour.

Experiment IV.—On May 21, 1891, a number (not counted) of larval Flounders in process of metamorphosis, procured from Mevagissey Harbour, were placed in the wooden tank with glass bottom previously described. The tank was divided into two equal parts by a wooden partition, and these larvæ were placed by themselves in the left-hand compartment.

On August 6, there were ten of this lot left alive, several having killed themselves by getting fixed in crevices. These ten survivors continually sought the dark corners of the tank, and remained with their lower sides in contact with the wooden sides, so that the lower sides of the Fish were by no means always exposed to the light coming through the glass bottom. Nevertheless, many of them at the date mentioned had some pigment on their lower sides.

On September 4, two of this lot of Fish died owing to an accidental stoppage of the circulation in the tank. I had placed some of the Fish in a glass bottle standing on the glass bottom of the tank in order that they might be constantly exposed to the light from below, and, when the circulation stopped, those in the bottle suffered more than those outside it, because they were in a smaller quantity of water. The larger of these two was 6·7 centims. long, and had pigment along the region of the fin-muscle on the lower side; the argenteum was developed in the peritoneum, and slightly in the skin of the abdominal region, but nowhere else. The smaller specimen was 4·3 centims. long, and had less pigment; there were in it only scattered chromatophores in the same region as in the other specimen; the argenteum was developed in the peritoneum, but not elsewhere on the lower side.

On September 10, I arranged a bell-jar over the mirror underneath the glass-bottom tank, fitted it with a constant-level circulation, and transferred to it the eight remaining Flounders of this year's brood. The reason of this was that in the wooden tank they persisted in clinging to the opaque sides. In the bell-jar, the lower sides were constantly exposed to the light. At this time, the majority of these Fish had no pigment on the lower sides, others had a little in the region of the muscles of the longitudinal fins.

In the following months, pigment developed very considerably on the lower sides of these specimens. The amount of pigment present was not definitely noted until February, 1892, although the Fish were regularly fed and tended. All this time it should be remembered the Fish were exposed to light both above and below, as no steps were taken to cover the sides of the bell-jar.

On February 13, 1892, one of the Flounders died. This death was, as usual, due to an accident. The outflow from the bell-jar was obstructed, the water overflowed at the top, and several of the Fish escaped; these were exposed for a time to the air on the floor, and one of them did not recover when restored to the water. This specimen was 8·7 centims. in length, and on its lower side pigment was strongly developed along the lateral line, and also in less quantity in the regions above and below the lateral line. There were also chromatophores along the edges of the head, and the edges of the body at the base of the tail. The argenteum was continuous over the abdominal region, absent at the bases of the fins, elsewhere developed only along the lines of the intermuscular septa. At this date, February 13, all of the seven surviving Flounders in this experiment except two, had some pigment on the lower sides.

On March 29, I removed these seven Flounders from the bell-jar, and put them into the left half of the glass-bottom tank, because I required the bell-jar in order to commence another experiment with new larval Flounders which I received on that day.

On May 12, one of the specimens died; it was one of the two in which no pigment could be seen on the lower side when it was alive in the tank. The results of an examination of the specimen were: It was 10·1 centims. long; on the lower side the argenteum was well developed, especially along the intermuscular septa. The amount of pigment on the lower side was very small; there was some at the extreme edges of the caudal portion of the body, between the longitudinal fins and the caudal fin, a small patch of chromatophores on the lower side of the caudal fin, and on the extremity of the lower pectoral.

On June 1, owing to renewed difficulty with the circulation in the glass-bottom tank, five more of the specimens in this experiment died, only one being left alive. The condition of these five was as follows:—

(1.) Length 12·4 centims., pigmented all over the lower side, except the head and extreme caudal region.

(2.) Length 11·3 centims., pigment less continuous, but still covering nearly the whole side.

(3.) 11·6 centims., same as (2), but a little less pigment.

(4.) 9·9 centims., same as (3).

(5.) 7·6 centims., pigment only in small patches.

The last surviving specimen of this experiment was pigmented at this date, and is now (September 29, 1892), about 23 centims. long, and pigmented over all the lower side except the head and caudal portion; it exhibits, in fact, more pigmentation than is shown in the figure.

The features of this experiment then briefly recapitulated are: Fish in glass-bottom tank from period of metamorphosis in May to August 6, 1891, when only ten survived, of which some had a little pigment on lower side. Two died on September 4, and showed a little pigment in the fin-muscle area. On September 10, remaining eight Fish transferred to a bell-jar, and illuminated both from above and below. On February 13, 1892, one specimen died, showing pigment considerably developed on its lower side. On March 29, the remaining seven specimens were removed to the tank with glass bottom, where the lower sides were constantly illuminated. On May 12, another specimen died; it showed scarcely any pigment on lower side. On June 1, five died; and one is still alive, all these six exhibiting a great deal of pigmentation on the lower side. Thus, pigment developed to a very marked extent in seven out of a total of eight specimens between September 10, 1891, and June 1, 1892, and I have little doubt that the specimen which died on May 12 would have developed pigment if it had lived a few months longer.

The general results, which I observe in these experiments, are the following: When, as in the first experiment, a number of young Flounders have been exposed for about four months, pigment is found to be developed on the lower side in a small proportion of them in the region of the fin-muscles, and these specimens are usually the smallest of the lot, with occasional exceptions. When the water in the apparatus becomes accidentally foul, the smaller pigmented specimens usually succumb, while the larger Fish, in which no pigment, or scarcely any, has appeared, survive. For instance, in Experiment IV., on September 4, 1891, two specimens died, both of which had pigment in the fin-muscle region, while the majority of the remaining eight had not yet developed pigment. As time goes on, the number of specimens in which pigment is present on the lower side continually increases. Thus, in Experiment IV., on February 13, 1892, one specimen died in which pigment was considerably developed, while all the rest, except two, were pigmented. On May 12, another specimen died, which had scarcely any pigment on the lower side, but all the remaining seven had developed pigment very strongly by June 1. I have noticed that where the pigment is only developed after the Fish has been exposed a long time, and after the argenteum has developed, it does not usually begin to appear, as in the younger specimens, in the fin-muscle region, but in the region of the trunk-muscles above and below the lateral line. The head and caudal region are always the last to develop pigment.

All the experiments prove clearly that the amount of pigment produced increases steadily with the duration of the exposure; but a comparison of Experiments IV. and II. shows that there is not so much difference as might have been expected between the results produced by commencing the exposure in the larval stage, and commencing it nearly four months after the metamorphosis. In the former case, pigment had appeared in some specimens in less than four months after the commencement of the exposure, and had appeared in all the surviving specimens, six out of ten, at the end of twelve months. In the latter case, pigment did not appear on any of the specimens until the exposure had lasted seven months; but it had appeared on all the specimens that lived long enough, three out of four, at the end of fourteen months. It is evident from this comparison that the development of the pigment is not connected with a particular age of the Fish, for in the latter case, although the duration of exposure was about the same as in Experiment IV., the age of the Fish was greater than the period of exposure by four months; so that whereas, in Experiment IV., pigment first appeared in specimens only about five or six months old, in Experiment II. it first appeared in specimens which were twelve months old.

One other conspicuous feature of the experiments is the great individual variation among the specimens in their susceptibility to the pigment-producing influence of light.

Having examined the anatomy and development of the elements of coloration in Pleuronectidæ and other Fishes, and the chemical and physical properties of the substances which characterize those elements, we are in a position to offer some interpretation of the experiments described, and to inquire into the causes of some of the phenomena of coloration in Fishes.

Examination of the specimens of Flounder in which coloration was produced on the lower side in these experiments, showed that the coloration was exactly of the same kind as that of the upper side in normal specimens. Wherever the skin was coloured there were both black and yellow chromatophores, not only superficially close beneath the epidermis, but also on the inner side of the skin. It was also found that, where the colour was well developed, the internal deposit of guanin, the argenteum, was scanty, as on the coloured side. We have no exact data to prove that, when colour is produced in a Fish of considerable size, in which the argenteum was fully developed before the pigmentation appeared, the guanin is absorbed, although it seems very probable. The coloration produced on the lower side further resembled that normally present on the upper in exhibiting changes of tint or intensity, being at one time very much darker than at another, under the influence of certain conditions. We have not made a special investigation of these changes, but we can assert that they are, like those of the upper side, due to dilatation and contraction of the chromatophores. Probably the condition of the latter is affected by the amount and kind of light falling upon the eyes of the Fish. Some light enters the dorsal or left eye of the Fish obliquely as it lies upon the glass bottom of the vessel, the axis of that eye being capable of being directed outward and downward; and other light enters both eyes after reflection from the top and sides of the vessel, for even black cloth does not absorb all the light that falls upon it. The amount of light thus affecting the eyes depends on the amount passing through the window, the surroundings of the Fish being constant. The exact relation between the temporary changes of coloration on the lower side and the light has not been observed, but it has been noticed that the tint of the lower side is not dark enough to harmonise with the black background against which it is seen. The most striking change which has been noticed is the extreme pallor of the colour of the lower side when the supply of water to the vessel accidentally fails for a time. The water being no longer renewed, the Fish soon suffer from a deficiency of oxygen, and are found breathing hurriedly and painfully, while the coloured parts of the lower side are a straw-coloured yellow instead of dark yellowish brown. When the circulation is restored, and the Fish recover from their semi-suffocation, the chromatophores of the lower side again dilate, and the normal colour reappears. The same pallor, but to a less degree, appears when the Fish are frightened and disturbed by a person lifting up the cover to look into the vessel from above.

Here may be mentioned some observations made in the course of these investigations which show that the chromotaphores of normal Flat Fishes are affected directly by mechanical stimulation, as, *à priori*, might be expected. When Flat Fishes are thrown into a basket as they are captured, and left to lie one upon the other for some hours until they are dead, or nearly so, it is found when they are taken out again that the upper sides are curiously marbled, areas of very irregular shape being very pale while neighbouring areas are very dark, and the boundary between the differently coloured areas being very sharp and distinct. On the other hand, if a Plaice or Flounder is taken alive from the water and allowed to die by itself with its upper side fully exposed, it invariably grows gradually darker, until when dead it is almost black. We have never observed pallor appearing as the consequence of the moribund condition in Fish dying in the usual way when taken out of the water, if they were left exposed. POUCHET[*] considers that general pallor, or the appearance of pale livid marks, is the consequence of the moribund condition in all cases, but as he remarks that his observations were made in the market of Concarneau, it is evident that he was referring to the curious marbling we have mentioned as appearing in Fish which have been partially covered. We at first thought that the contraction of the chromatophores in this case was due to the exclusion of light, but this seemed improbable because the exclusion of light in the living Fish usually causes the chromatophores to expand. It was observed, however, that in a piece of fresh skin partly covered by a cover-glass on a glass slide, the chromatophores under the cover-glass became contracted while those in the uncovered skin remained expanded. It was inferred from this that contact with a solid subject and slight pressure were the cause of the contraction, and this was easily proved to be true, for the course of the end of a glass rod drawn along the surface of the skin of a Plaice or Flounder became visible in a few minutes as a light streak on a dark background. In a Fish removed from the water and rapidly dying, the chromatophores remain alive after the Fish is dead, or nearly so, and so retain their contractility unaffected by influences from the nervous system. In this condition they contract if anything rests upon the skin, and when they themselves are dead they remain permanently contracted; on the other hand, if left to themselves they gradually expand as the Fish dies and as they die themselves. This is the explanation of the mottled or marbled appearance of Fish which have been packed one upon another while still alive.

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[*] 'Changements de Coloration, etc.,' p. 33.

IV.—ABNORMALITIES OF COLORATION IN PLEURONECTIDÆ OCCURRING IN NATURE.

The experiments described in the previous section seem to indicate that the action of daylight determines the appearance of black and yellow chromatophores in the skin of the lower sides of Flounders, and the absorption of guanin deposits. But it must be remembered that specimens abnormally coloured are of not infrequent occurrence in various species of Flat Fishes. Every naturalist who has paid attention to the Pleuronectidæ has met with such abnormal specimens. The abnormalities are of various kinds and degrees. The commonest and least conspicuous is the mere reversal of the asymmetry which is characteristic of the species, the differences between the two sides being the same as in normal specimens, but the left side presenting the characters usually connected with the right, and *vice versâ*. According to my own experience, this variation is most frequent in the Flounder, *Pleuronectes flesus;* in the neighbourhood of Plymouth a large percentage of Flounders are sinistral instead of dextral.

It is a curious fact that in a sinistral Flat Fish, whether it is normally sinistral like the Turbot, or abnormally like a reversed Flounder, the viscera are in the same position as in a dextral specimen ; the liver is on the left side, the coils of the intestine on the right. The reversal of the relations of the two sides externally does not affect the relations of the internal organs, which remain constant.

But more important in relation to the subject of the present memoir are abnormalities of coloration, which consist in the presence of some pigment, from small patches up to complete pigmentation, on the lower side of the Fish, or the absence of pigment from part or from the whole of the ocular side.

Specimens which are pigmented all over the lower side as well as the upper, or ocular, have usually been called double, but, as this term is evidently not quite suitable, we prefer the term "ambicolorate." An abnormality of the head is frequently found in ambicolorate specimens; in this abnormality the anterior end of the dorsal fin, instead of extending forwards towards the snout on the outer side of the dorsal eye, terminates behind the level of the eyes, and its end forms a curved hook projecting forwards, as shown in Plate 54, fig. 1.

Before referring to the descriptions of such abnormalities previously published, we shall proceed to enumerate the specimens that have come under our own notice or been described to us by other naturalists. The following specimens were collected at Plymouth :—

Pleuronectes flesus.—(1.) 7⅝ inches in length. Almost entirely coloured on the lower side as well as on the upper.

Anterior end of the dorsal fin with a base forming a hook projecting over the dorsal (left) eye, which is on the edge of the head, and partly visible from the lower side.

Dorsal and ventral tubercles developed on the lower side as on the upper, but no rough scales on the lateral line on the lower side, very few on the upper.

The exact appearance of this specimen after preservation in spirit is represented in figs. 1 and 2, Plate 54, which are drawn of the natural size. The coloration is somewhat obscured by the coagulation of the tissues, due to the spirit, especially by the coagulated epidermis. It is noteworthy that the correlation between coloration and structural deformity, which we notice below in the Turbot, does not hold for the Flounder. The yellowish white part of the skin at the base of the tail is the only part of the lower side where the argenteum is normally developed, over the rest of the lower side it is almost entirely absent, as it is on the upper pigmented side in normal specimens. This is an instance of the inverse relation between pigment and guanin, which we discuss in other parts of this memoir.

(2.) Length, 13¼ inches; sex, female. Completely coloured on both sides, but the colour of the left side not quite so intense as that of the right.

Anterior end of the dorsal fin hooked, base terminating behind the left eye; left eye rather on the upper side of the head than on the edge.

Dorsal and ventral tubercles on the lower side as well as on the upper, and rough scales on lateral line on lower side also.

(3.) 11⅝ inches long. Completely ambicolorate, dorsal fin hooked-shaped anteriorly. Tubercles on lower side as on upper, few rough scales on lateral line on upper side, only one or two on lower.

(4.) 8¼ inches long. Completely ambicolorate, dorsal fin hooked-shaped anteriorly. Tubercles on lower side as on upper, but few rough scales on lateral line.

(5.) 12⅝ inches long. Small spots of colour irregularly scattered over lower side, dorsal fin and head normal. No tubercles on lower side, but where one of the coloured spots covered the lateral line anteriorly there were a few rough scales.

Pleuronectes microcephalus.—(1.) 13 inches long. Coloured continuously over lower side, as on upper, except an area extending a little beyond the head, which was white. No abnormality in structure. Sex, male.

(2.) 11¾ inches long. Similar to the preceding, but the outline of the anterior white region on the lower side was not so definitely marked. Sex, male.

Pleuronectes platessa.—A specimen about 10 inches long, in which the posterior two-thirds of the lower side are continuously coloured like the upper side, but the anterior third is white. The anterior end of the dorsal fin is not quite normal, the base of attachment terminating behind the eyes, although the end of the fin itself does not project into a prominent hook.

Solea vulgaris.—12 inches long. Male. Lower side white as in normal specimens, upper side almost all white also. The only pigmented parts of the ocular side are the head from the edge of the operculum forwards, the pigmentation extending beyond the head only in a small spot above the base of the pelvic fin, and the distal [illegible] the tail. The rest of the upper side is entirely destitute of pigment, and over this area the argenteum, usually rudimentary on the upper side, is as much developed as on the lower side.

The fish merchant who gave this specimen, asked if the explanation of its condition might be that it had been skinned when captured and then been thrown overboard alive and had recovered, the white upper side showing where the flayed surface had healed over! The suggestion cannot, of course, be entertained. The skin of the upper side is normal, and contains normal scales.

The following specimens were sent to Mr. CUNNINGHAM by Mr. E. W. L. HOLT, who collected them from trawlers at Grimsby.

Rhombus maximus.—(1.) 23¾ inches long. Female. The whole of the lower (right) side coloured like the upper, except part of the lower side of the head. The skin of the lower jaw was pigmented on the lower side, and the coloration extended forwards as far as the preopercular bone; the rest of this side of the head was white. Tubercles in the skin on the lower side as on the upper, but on the head they were fewer in number and smaller than on the upper side; the projecting points of these tubercles were worn down on the lower side, and slightly worn on the upper side also. Attachment of dorsal fin terminated behind the eyes and the fin projected over the right eye in the form of a hook. A little pigment in the peritoneum both of the lower side and the upper.

(2.) 20⅞ inches. Female. Condition very similar to that of preceding specimen. Lower jaw and anterior end of dorsal fin pigmented, rest of head white in front of the preopercular bone. Dermal tubercles on the lower side much worn. Peritoneum slightly pigmented both on upper and lower side. Dorsal fin hook-shaped anteriorly.

(3.) 16½ inches. Female. Condition very similar. Distal half of lower jaw on lower side pigmented, and all the rest of the lower side, except the head, in front of preopercular. Lower pectoral fin edged with white. Peritoneum slightly pigmented both above and below. Dorsal fin hook-shaped anteriorly.

(4.) 14 inches. Male. Coloured on both sides entirely. Tubercles on lower side not so numerous or so large as on upper. Dorsal eye near edge of head but not directed horizontally. Peritoneum slightly pigmented both above and below. Dorsal fin hook-shaped anteriorly.

(5.) 13 inches. Female. Coloured all over lower side except side of the head in front of preopercular and lower jaw; anterior end of dorsal fin coloured. Dorsal eye on the edge of the head, and directed horizontally. Peritoneum pigmented above and below. Dorsal fin hook-shaped anteriorly.

(6.) 11⅞ inches. Similar to preceding; head on lower side unpigmented in front of preopercular, lower jaw and anterior end of dorsal fin pigmented. Dorsal fin hook-shaped anteriorly.

(7.) 19½ inches. Female. Coloured over the whole of the lower side except head in front of preoperculum: tubercles also on lower side of body, but none on the head. Differs from the others in the absence of pigment from the lower side of the lower jaw, and from the anterior end of the dorsal fin, also in the fact that the head, eyes, and dorsal fin are *perfectly normal in structure.*

Pleuronectes platessa.—19¾ inches long. Female. The head normal, and lower side white as in normal specimens. Anterior end of upper side pigmented, and also the posterior third, but the rest of the upper side white like the lower side. On the dorsal edge of the body there was a considerable indentation, somewhat behind the head, looking like a scar resulting from the healing of a deep incised wound. This indentation was nearly in the middle of the length of the body included in the white area of the upper side, a relation which suggests the possibility that the disappearance of the pigment had been caused by the injury; this, however, is not probable.

Mr. HOLT states that such piebald Plaice are common enough in the market at Grimsby.

We are indebted to Dr. G. H. FOWLER for some notes of abnormally coloured specimens of Plaice made by Dr. BRANDT at Kiel, and communicated with his consent. They are as follows:—

(1.) Lower side entirely pigmented; head with the typical abnormalities of eye and dorsal fin.

(2.) Lower side all pigmented, upper side normal.

(3.) Lower side irregularly blotched with pigment spots.

(4.) Lower side spotted white on dark (*i.e.*, pigmented area larger than the white), very closely and evenly. Upper side irregularly blotched with white.

(5.) Lower side with two dark longitudinal streaks along the edges; upper side normal.

(6.) Lower side with a very dark posterior half, and antero-ventral patch; remainder white. Upper side normal.

(7.) Lower side quite dark, except head and pectoral fin, which are quite white, and the dorsal and ventral fins, which are mottled. Upper side normal. *Reversed.*

(8.) Lower side very slightly spotted; upper side with a circular light patch, three inches in diameter.

(9, 10.) Lower side normal. Upper side, dorsal and ventral fins quite white, except one or two pigmented patches; tail fin piebald.

(11.) Lower side spotted with pigment on body and mottled on fins. Upper side mottled with white on head and anterior region.

(12.) Lower side normal. Upper side, a white patch behind the head from pectoral fin to dorsal edge.

(13, 14.) Lower side with a few very small spots. Upper side quite white all over, except a few scattered spots of pigment.

(15.) The same as preceding, but no spots on lower side.

Among the specimens included in the above list the malformation of the head, accompanied by complete or nearly complete ambicoloration, occurs most frequently in the Turbot, namely, in six specimens. There are three specimens of the Flounder showing the same condition, and two of the Plaice, in one of which the malformation is incompletely developed. We have not yet met with, or heard of, any instances of this malformation in the Merry Sole (or Lemon Sole, *Pleuronectes microcephalus*[*]) or in the Dab (*P. limanda*), or in the genera *Solea, Arnoglossus, Zeugopterus, Hippoglossus*, or *Hippoglossoides*.

Cases of this malformation of the head have been frequently mentioned and described by ichthyologists. The first reference to it is that of DONOVAN,[†] who describes an instance of it in the Turbot as type of a distinct species, *Pleuronectes cyclops*. YARRELL[‡] mentions and figures the malformation in a Brill. COUCH[§] describes and figures it in the Flounder, in which species, he says, it is so common in some districts "as to have raised the suspicion of its being truly a distinct species." HIGGINS[||] mentions it in the Flounder, naming the specimen *Platessa melanogaster*, and it is also recorded in the same species by THOMPSON[¶] and by RITZEMA BOS.[**] DAY states[††] that, according to R. COUCH, *Zeugopterus punctatus* is "very subject to malformation of the anterior end of the dorsal fin, causing it to form an arch over the eyes;" but as he gives no reference, he was probably quoting a verbal communication, and this cannot be regarded as sufficient evidence that the malformation here considered has been observed in this species. So far as we can discover, it has not been mentioned in connection with any other species besides the Turbot, Brill, and Flounder, so that our observations of its occurrence in the Plaice is the first on record, and here it must be noted that in the specimen seen at Plymouth the malformation is not fully developed, and the only other specimen, observed at Kiel, is mentioned on the authority of Dr. FOWLER. On the other hand, DAY[‡‡] states that he obtained from Brixham a double Sole, 11½ inches in length, with the eyes placed as normally in this species. So that it would appear that, even when the lower side is coloured in the Sole, no malformation of the head occurs. The two ambicolorate specimens of *P. microcephalus* mentioned in our list had as much pigmentation on the lower side as the Turbot, in which the malformation is present, and yet there is no malformation in them.

The evidence at present available then tends to prove that the malformation of the head occurs in ambicolorate specimens of *Rhombus maximus, R. lævis, Pleuronectes flesus*, and less frequently in *P. platessa*, but not in other species. It is natural to inquire whether these species differ from the rest of the family in any particulars of habit, development, or structure, which might in some way be connected with the occurrence of this malformation. With respect to development the Turbot and Brill are provided in the larval condition with an air bladder, and remain almost entirely pelagic until the metamorphosis is very nearly complete. The young of this species are found in summer swimming at the surface until the eye is at the edge of the head or even partly on the left side. In this intermediate condition they do not swim vertically, but in a slanting, oblique position, but the retention of the pelagic habit for so long a time might be supposed to be in some way connected with the frequent occurrence of the malformation, were it not that the Flounder abandons the pelagic habit as early as any member of the family, and does not resemble the Turbot in this respect at all. On the other hand, the Sole, as Mr. CUNNINGHAM has shown,* has an air bladder in its intermediate condition, although it is not often found at the very surface of the sea, and it does not exhibit this occasional malformation.

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[*] Mr. HOLT informs us that he has seen the malformation partially developed in Lemon Sole.

[†] 'Brit. Fishes,' vol. 4, Plate 90.

[‡] 'Brit. Fishes,' 1836, vol. 2, p. 242.

[§] 'Brit. Fishes,' 1864, vol. 3, p. 198.

[||] 'Zoologist,' 1855, vol. 13, p. 4596.

[¶] 'Proc. Zool. Soc.,' 1837, p. 60.

[**] 'Biol. Centralbl.,' vol. 6, p. 270.

[††] 'Brit. Fishes,' 1884, vol. 2, p. 19.

[‡‡] *Op. cit.*, vol. 2, p. 40.

Then, again, it might be suggested that the species which pass the first part of their lives near the shore are subject to this malformation, but the young of the Sole has only been taken near the shore, and agrees in its habits with the Turbot more than does the Flounder.

Lastly, it is evident that the occurrence of the malformation does not correspond to the degree of anterior extension of the dorsal fin, characteristic of the species, for this is greater in the Sole, and much less in the Flounder than in the Turbot.

But although we are unable to discover at present a correlation between the occurrence of this malformation and any peculiarity of the species in which it occurs, there is a distinct correlation in the individual Turbot between the structural malformation and the degree of pigmentation of the lower side. We have been unable to find any evidence that a specimen of Turbot, Brill, Flounder, or Plaice has ever been observed in which the whole of the lower side was continuously pigmented, and yet the structure of the head was normal. In other words, complete ambicoloration in these species is always accompanied by the typical malformation of the head and dorsal fin. Conversely, when this structural malformation is present the lower side of the Fish is always completely or nearly completely pigmented. In the case of the Turbot it is interesting to notice the limit of this correlation between structure and coloration. Thus, of the Turbot in the above list, only one, the fourth in the list, is pigmented over the whole of the lower side, and in this, of course, the malformation occurs; in the other five in which the malformation is present, pigment is absent from the lower side of the head in front of the preoperculum, but present on the lower side of the lower jaw and of the anterior end of the dorsal fin and its neighbourhood. In the seventh specimen in the list the pigmentation has the same extent except that it is not present on the lower side of the lower jaw, nor on the anterior region of the dorsal fin; and in this specimen there is no structural malformation. Thus it would seem that if we draw an imaginary line through the preopercular bone in the Turbot, pigmentation may extend over the whole of the lower side behind this line without any structural malformation being present, but when pigment is also present on the lower side in front of this line the characteristic structural malformation occurs also; on the other hand the structural malformation has never been observed in any specimens in which the lower side was unpigmented or pigmented to a less extent than that defined above.

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* 'Journ. Mar. Biol. Assn.,' 2, 4.

Mr. HOLT has sent us a description of a Brill about ten inches long in his possession, alive, in which there is a slight notch beneath the anterior end of the dorsal fin, but the eyes are normal and there is no colour on the lower side except a very small spot above the nasal valve of the right side just behind the notch. His sketch showed that this is not a case of the so-called cyclopean malformation which we have been considering. In the latter the attachment of the dorsal fin ends anteriorly some distance behind the dorsal eye, in Mr. HOLT'S Brill, the attachment is continued forwards to a point about $\frac{1}{8}$ inch in front of the anterior margin of the dorsal eye, and the free portion of the base of the fin is only $\frac{1}{4}$ inch long instead of $\frac{3}{4}$ inch or more, as in the typical case. The difference is one of degree, it is true, but it is a very great difference of degree, and does not contradict the conclusions we have formulated as to the correlation of the typical malformation with ambicoloration.

The occurrence of spots of pigment on the lower side, in a series along each border in the region of the muscles of the longitudinal fins, is very common in the Turbot and Brill. We have seen numerous specimens of the Brill exhibiting such spots, which are few in number and of considerable size, and GIARD points out that the piebald coloration of the lower side was considered by earlier French ichthyologists (DAUBENTON, BONNATERRE, LACÉPÈDE) as a specific character of *Rhombus maximus.*

It has often been stated without proof that these abnormalities of coloration are due to an abnormal exposure to light of the specimens in which they occur. But we have been unable to find any evidence in support of such statements. No reliable observations are on record of abnormal habits exhibited by these abnormal Fish, or of their existence under abnormal conditions. Mr. CUNNINGHAM has kept an abnormal specimen of the Plaice alive and under observation at the aquarium at Plymouth, from September 19, 1891, up to the present time. This specimen is the one mentioned above as coloured over three-fourths of the lower side on the same way as in the upper, the anterior fourth of the lower side being white as in normal specimens. The anterior end of the dorsal fin was not normal nor yet so abnormal as in typical "cyclopean" specimens, it terminated abruptly behind the level of the dorsal eye without projecting into a hook. This specimen was exceedingly shy and timid, and always remained completely buried in the sand at the bottom of the tank. It was never observed to swim of its own accord, and when dislodged from the sand, it swam horizontally like a normal Plaice and buried itself with violent movements of its fins as soon as possible. Moreover, it has exhibited not the slightest diminution in the coloration of the lower side since the day on which it was first brought to the aquarium, although its lower side has not since that time been exposed to the light any more than in the case of normal specimens.

Again, Professor GIARD has suggested that the malformed or monstrous ambicolorate specimens do not swim all their lives vertically, but that they remain longer in that position than normal specimens, "in any case long enough to allow the influence of the light to act efficaciously on the side ordinarily colourless." In fact, if I understand him rightly* GIARD's proposed explanation of the condition of the monstrous Turbot is this:—The Turbot has a long period of metamorphosis during which it is pelagic; in consequence of this it is liable to have its normal metamorphosis arrested and altered, and in this case its eye does not pass completely into its proper position, and the relations of the end of the dorsal fin become abnormal. A specimen so affected remains pelagic for a longer time than usual, the right side is exposed to light for a longer time than usual, and in consequence remains pigmented instead of becoming white and unpigmented.

Now if the presence of pigment on the right side of the monstrous Turbot is to be explained in this way, all other abnormalities of coloration in Flat Fishes ought also to be explained as due to the action of light. But even GIARD himself does not suggest that the occurrence of pigmentation on the lower side, or its absence on the upper side of specimens structurally normal are due to abnormal conditions to which these specimens were exposed. We have not the slightest evidence at present that these abnormal specimens have been exposed to abnormal conditions or have had abnormal habits of life.

These abnormalities of coloration in Flat Fishes, when carefully considered, give rise to some very interesting speculations. We will take, first, cases of pigmentation on the lower side which is normally unpigmented. If the presence of the pigment is due to an unusual exposure of the lower side to light, then, of course, the phenomenon is of the same kind as that shown in Mr. CUNNINGHAM's experiment, the pigment is an acquired character produced by the action of the environment on the individual. But suppose that it is independent of the action of light, then it is a congenital variation, independent of the action of the environment on the individual. The question then arises: is it a case of reversion or atavism, as it is generally assumed to be? Now it is clear that ambicoloration cannot be simply reversion, because we must necessarily suppose that the symmetrical vertically swimming ancestor of the Flat Fish had an unpigmented, white or silvery ventral surface, as other symmetrical Fishes have, it could not have been uniformly pigmented all over, as a completely ambicolorate Flat Fish is. Therefore the explanation, the comprehension of this common variation, is a much more difficult and complicated matter than it seems to be at first. We may suppose that the hereditary tendency leading to reversion has been modified by a tendency of the lower side of the Fish to resemble the upper; or we may suppose that there is no reversion in the matter at all, but that there is some occult tendency, in certain individuals, of the lower side to imitate the upper. It is a curious and remarkable fact that there is no tendency shown in Flat-Fishes to develop pigment on the dorsal halves of both sides whilst it is absent from the ventral halves.

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* [illegible] "Sur la Persistance partielle de la Symétrie Bilatérale chez un Turbot, &c." 'C. R. Soc. de [illegible] 1892, and 'Natural Science,' I. 5, p. 358.

An interesting fact is the distribution of pigment in the peritoneum in normal Flat Fishes. In some Fishes the colour of the peritoneum has an effect on the external appearance, because it is visible through the thin translucent body-walls. Even in Pleuronectidæ in certain species, and in certain stages of other species, the reflecting opaque tissue of the peritoneum of the lower side is visible from the exterior when there is little or no argenteum in the skin. But the fact is, that the peritoneum of the upper side in normal Pleuronectidæ is black, while that of the lower side contains little or no pigment, but contains more argenteum or more guanin than that of the upper. Now the peritoneum is of small extent compared with the whole of the lower side, and it can scarcely be maintained that the appearance of its argenteum from the exterior is of any use or advantage to the Fish, while the pigmentation of the peritoneum of the upper side adds nothing at all to the external appearance of the upper side. Fig. 8, Plate 55, shows the appearance of the peritoneum of the ovarian pouch of the upper side in the *Pleuronectes microcephalus*, a network of black chromatophores resting on a granular deposit of granules of guanin; no "coloured" pigment was present. In the corresponding portion of the lower side there were two or three minute black chromatophores in the same area. This difference can only be explained as the effect of light falling on the upper side of the Fish, and not on the lower.

We have written of Flat Fishes in general as having no pigment on the lower sides, but the subject is still further complicated by the fact that in certain species there is normally some pigment on the lower side. We have already referred to the frequent occurrence of dorsal and ventral spots on the lower side of the Turbot and Brill; but Mr. HOLT has kindly brought to our notice the fact that in normal specimens of the Witch or Pole Dab, *Pleuronectes cynoglossus*, the lower side is not white but grey. He sent us four specimens of this species, and we found that the superficial layer of the skin, outside the scales, contained a layer of closely crowded iridocytes, and large radiate black chromatophores uniformly distributed over the whole surface, but not very close together. There were, however, no coloured chromatophores, no lipochrome was present, although on the upper side orange chromatophores were present as usual. The internal layer of the skin on the lower side contained neither argenteum nor chromatophores. In this species the colour of the upper side is not so deep as in the Plaice, Flounder, or Turbot, and both upper and lower sides are more pigmented in larger than in smaller specimens. It should be noted that this species belongs to deeper water than the Plaice, Flounder, Turbot, and other species. Its young have not been found at less depths than 80 fathoms, and the adult has been taken at all depths up to 700 fathoms. Perhaps the peculiarity is related to the fact that light at greater depths is more dispersed than in shallow water, and therefore affects the

Fish more equally on the two sides. We do not know that the habits of the Fish expose the lower side more than usual, but any Flat Fish rises from the bottom occasionally, and in deep water, the light being more diffused, may affect the lower side more on these occasions. On the other hand, the explanation may be that this species became a Flat Fish more recently than others, and has, therefore, not advanced so far along the line of evolution of Pleuronectids, though we know of no evidence that this is so.

A species of Pleuronectid normally pigmented on the lower side has been described by JORDAN and BELLMAN ('Proc. U.S. National Museum,' vol. 12, p. 176). Several specimens of it were taken in 1887–1888 in the Pacific Ocean, off the coast of Columbia, at depths of 33 and 51½ fathoms. It is named *Engyophrys sancti-laurentii, nov. gen., nov. sp.* It is allied to *Platophrys*, SWAINSON, and *Engyprosopon*, GÜNTHER, but differs from all related species by the peculiar coloration of the blind sides. The colour of the left or eyed side is blackish brown, with scattered white and black spots, the latter most conspicuous along the bases of the longitudinal fins: three large black blotches on the straight part of the lateral line. Blind side with five or six curved, parallel, dusky bands as wide as the eye, the first beginning on the inter-opercular, and curving across the cheeks to along the base of the dorsal; second beginning at the throat, curving along the posterior margin of the preopercular, and extending along the dorsal region parallel to first; third curving round in front of the pectoral, across the posterior part of the opercular, and extending to the base of the dorsal fin behind the middle of the body: the others behind the pectoral. All of these bands fade out behind the middle of the body, so that the posterior portion is "immaculate," which appears to mean white and unpigmented. In young examples these bands are very faint or obsolete.

DESCRIPTION OF PLATES.

PLATE 53.

Condition, drawn from life, of the lower side of a specimen of Flounder (*Pleuronectes flesus*, GOTTSCHE), on November 13, 1891; this side having been exposed to daylight since September 17, 1890. The specimen was captured in May, 1890, when about 1·2 centim. long, and was reared in the aquarium under ordinary conditions until September 17. At this time, when the experiment was commenced, there was not a trace of pigment on the lower side. The Fish is represented at its natural size.

PLATE 54.

Fig. 1.—Lower side of an abnormal specimen of a Flounder captured in the trawl at sea. Drawn of the natural size after being preserved in spirit. The dark portions are pigmented, the bluish portion is the unpigmented skin coagulated by the spirit. The white portion at the base of the tail is the only part where the argenteum is fully developed.

Fig. 2.—Anterior portion of the upper side of the same specimen.

Fig. 3.—Appearance of a superficial slice of the skin of the upper side of a freshly-killed normal Flounder as seen under ZEISS CC., Oc. 3. Drawn with ABBE's camera lucida. The black and coloured spots are the chromatophores, the smaller grey plates are the iridocytes. Transmitted light.

Fig. 4.—Iridocytes in the superficial portion of the skin of the lower side in a freshly-killed Flounder. ZEISS CC., Oc. 3, camera. Transmitted light.

Fig. 5.—Iridocytes of the same kind more highly magnified. ZEISS E., Oc. 3.

Fig. 6.—Chromatophores and iridocytes in the superficial layer of the skin of the *lower* side of a Flounder which died in the experimental apparatus, July 4, 1892. The history of the specimen was the same as of that represented in Plate 53, but the skin was not examined until some hours after death, so that the pigment of the coloured chromatophores is somewhat faded and diffused.

PLATE 55.

Fig. 1.—Appearance of fresh skin of normal littoral specimen of *Cottus bubalis*, lateral region below posterior part of anterior dorsal fin. ZEISS A., Oc. 3.

Fig. 2.—Appearance of skin from same region of a red specimen, from deep water, of the same species.

Fig. 3.—Dorsal skin, fresh, of the brown Pipe-Fish, *Syngnathus acus*. ZEISS CC., Oc. 3. Transmitted light.

Fig. 4.—Dorsal skin, fresh, of the green Pipe-Fish, *Siphonostoma typhle*. ZEISS CC., Oc. 3. Transmitted light.

Fig 5.—Chromatophores in skin of pectoral fin of *Trigla cuculus*, the Red Gurnard. The red chromatophores contain tetronerythrin, the granules consist of guanin. Drawn some time after death. × 300.

Fig. 6.—Skin of *Trigla hirundo*, showing chromatophores and guanin granules. Drawn some time after death. × 300.

Fig. 7.—Chromatophores in skin of *Nerophis æquoreus*, the banded Pipe-Fish. Drawn some time after death.

Fig. 8.—Peritoneum of the upper side of *Pleuronectes microcephalus*, the Merry Sole or Lemon Dab. The granular layer is the reflecting tissue composed of guanin. On the lower side only this tissue is present, the network of black pigment is almost entirely absent.

Fig. 9.—Spherical masses composed of needles of guanin from skin of *Pleuronectes limanda*, the common Dab.

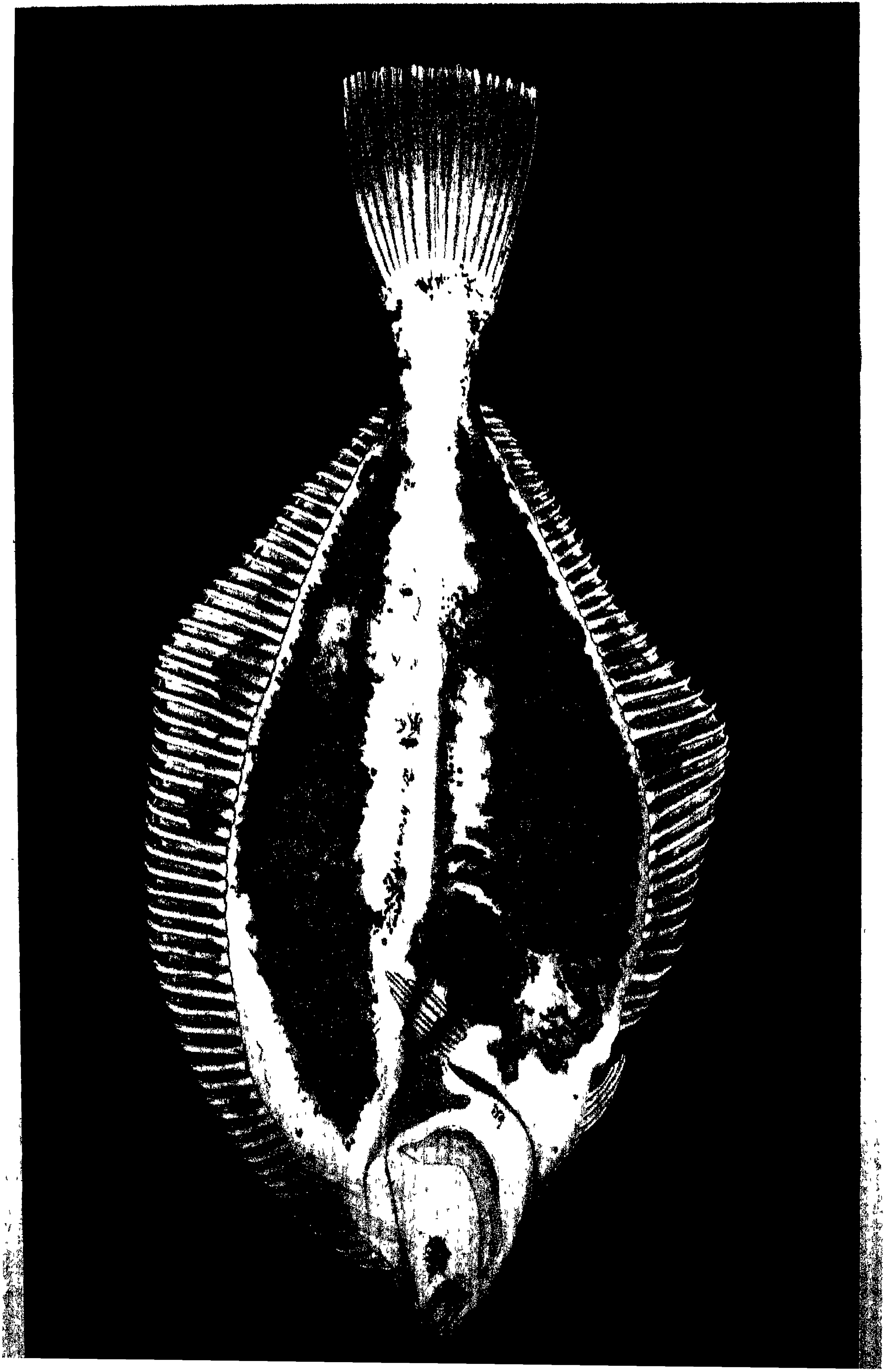
Fig. 10.—Reflecting tissue composed of bacilli from the ventral post-anal skin of *Siphonostoma typhle* outside the dermal scutes.

Fig. 11.—Rods from the silvery peritoneal layer of *Osmerus eperlanus:* guanin needles; *a*, in bundles; *b*, isolated. × 300.

Fig. 12.—Shows how the golden appearance is produced in the eye of a Fish, here from the argenteum of *Trigla hirundo*. A yellow lipochrome overlies a layer of guanin needles. × 300.

Fig. 13.—Isolated crystals of guanin from the silvery layer of the air-bladder of the Herring, prepared as described in the text. × 800.

Fig. 14.—Larger crystals from the same source. × 300.



PLEURONECTES FLESUS ACQUIRED PIGMENTATION

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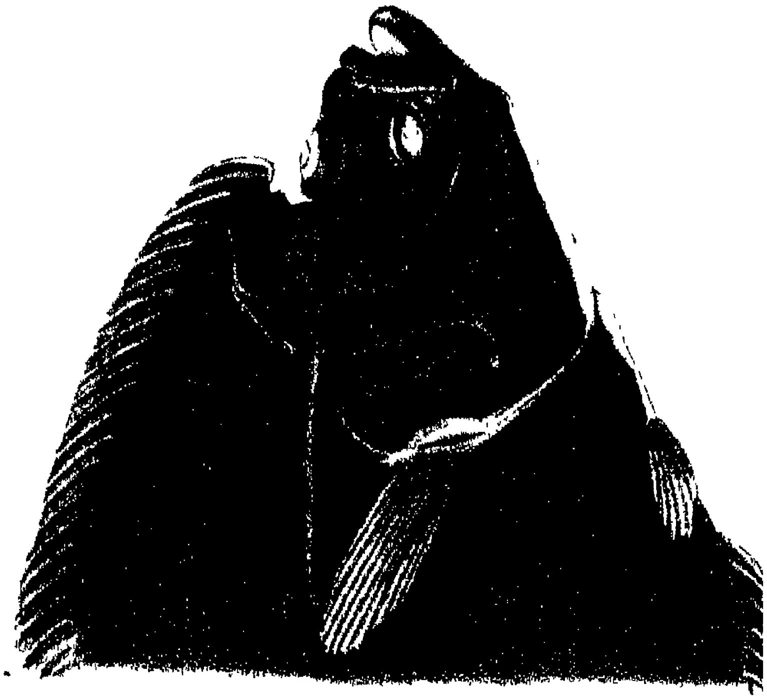

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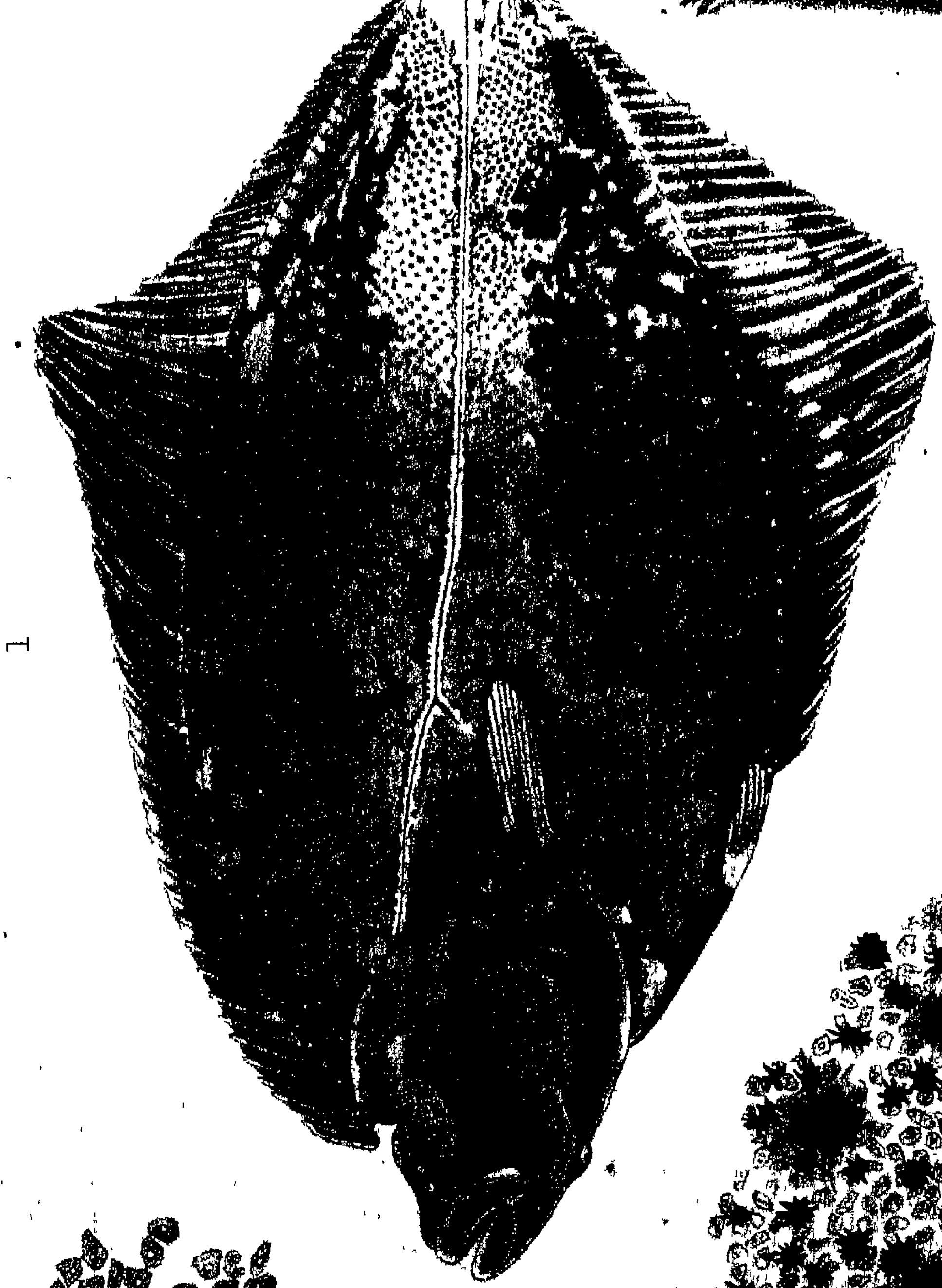

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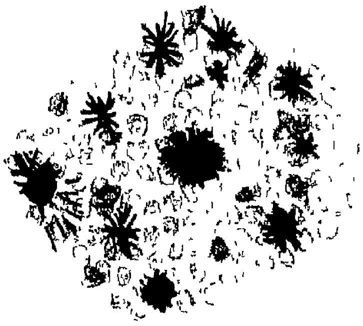

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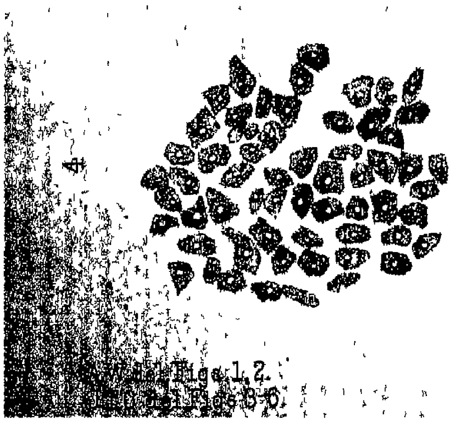

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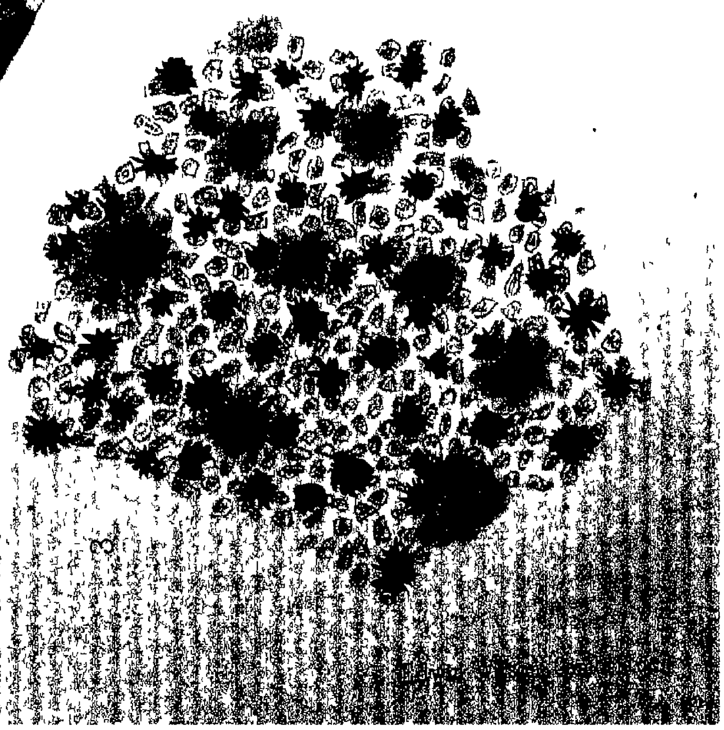

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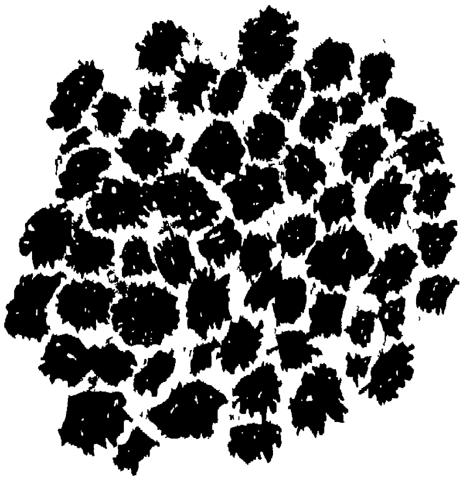

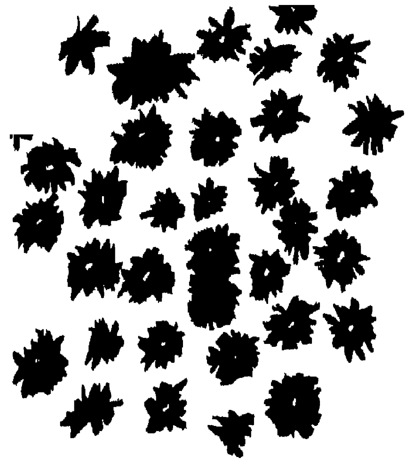

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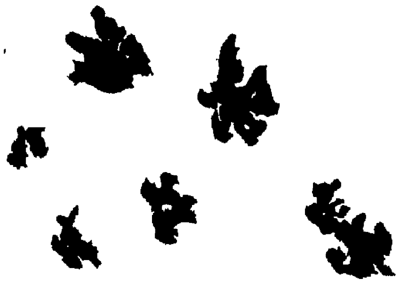

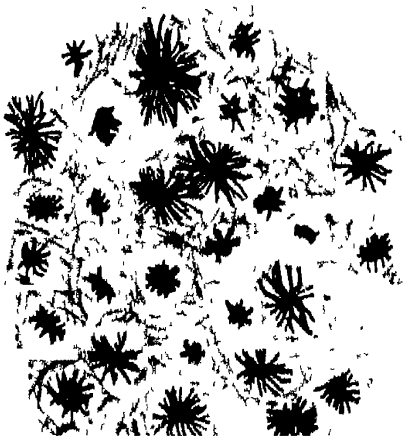

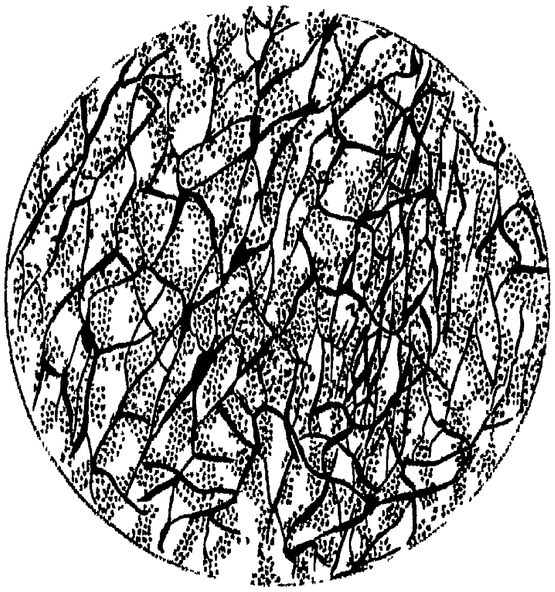

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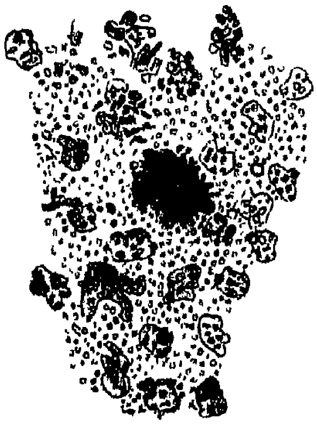

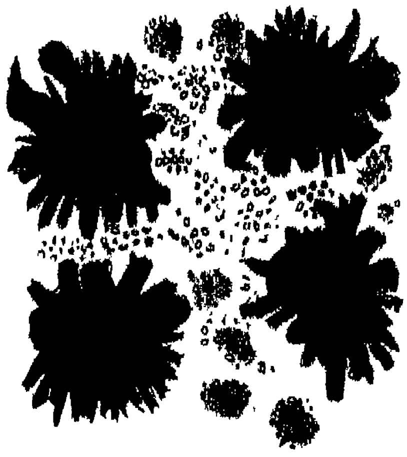

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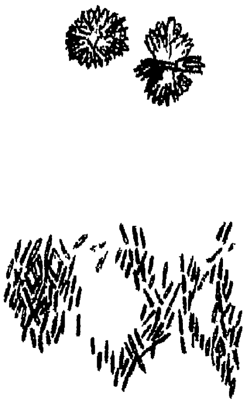

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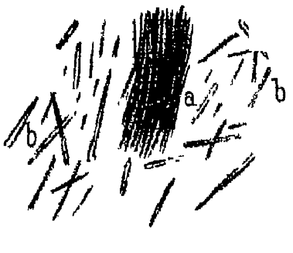

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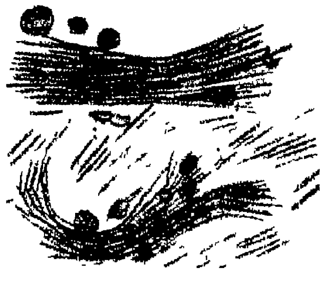

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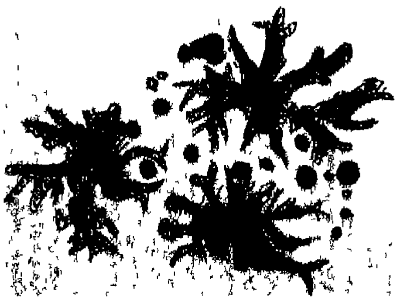

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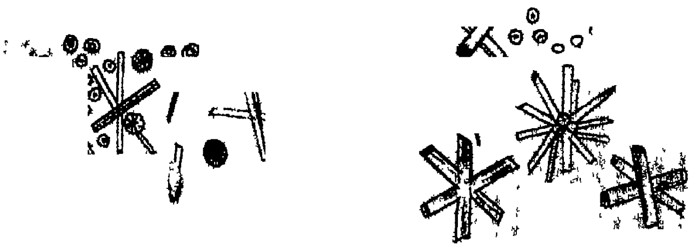

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Edwin Wilson Cambridge.

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